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A REVISION OF THE BRITISH SPECIES OF *CRYPTOPHAGUS* (HERBST) (COLEOPTERA: CRYPTOPHAGIDAE).

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INTRODUCTION.

In the past, three keys have been generally available to workers in Britain for the identification of species of *Cryptophagus* (Herbst). They are those of Fowler (1886-91), Chitty (1907), who followed Ganglbauer (1892-1904) and whose key was also used by Fowler and Donisthorpe (1913), and Joy (1932). In addition Reitter (1908-16) has been widely used and, more recently, Hinton (1945) has produced a key limited to those species which have been found associated with stored products. The writers, working independently, came to the conclusion that these keys were of little value for the accurate determination of the species of this extremely difficult genus, and have co-operated in producing this revision.

Hinton's key, which is of value only in a limited field, is based upon Bruce (1936), a work hitherto little known in this country. Bruce's monograph includes all the European species known to him, and is a work of very considerable value. For the first time the excellent characters of the male genitalia are used and this enables Bruce to clear up many long-standing misconceptions.

Bruce gives two keys, both based upon external morphological characters. The first is simple and easy to use, but relies to some extent upon highly variable

features and is consequently rather unreliable. An occasional error in logic occurs, as when (couplet 23) a decision that the pronotal puncturation is twice as strong as the elytral puncturation must be followed (couplet 25) by an estimate that the former is less strong than the latter in order to reach the determination *inaequalis* Reitter. Also, certain separations are obviously incorrect. For example, in all specimens of *obsoletus* Reitter which we have seen (about 100) the lateral tooth of the pronotum is clearly and constantly behind the middle of the pronotal side, and the callosity at the anterior angle has a small but distinct tooth (Coombs and Woodroffe, 1952a). This species can be correctly determined with Bruce's first key only if the lateral tooth is taken as being in the middle of the pronotal side and the callosity as not toothed.

Bruce's second key is an improvement on his first in that it allows, to some extent, for the extreme variability of many of the characters. Unfortunately, in achieving this, it has become extremely cumbersome and difficult to use. In one instance (couplet 3) one half of a couplet consists of four alternatives and the other half of three. When one is dealing with highly variable and poorly differentiated species separations of this degree of complexity are virtually unworkable. In defence of Bruce it must be emphasised that to produce a simple and accurate key to all European species of *Cryptophagus* is an almost impossible task unless the features of the male genitalia are used as key characters. The writers were fortunate in being able to limit their field to include only British species.

Classification.

There is considerable difference of opinion between authors as to the status of *Cryptophagus* (Herbst), *Micrambe* Thomson, *Mnionomus* Wollaston and *Micrambinus* Reitter. Falcoz (1929-31) treats *Micrambe* and *Cryptophagus* as genera, but considers *Mnionomus* and *Micrambinus* to be subgenera of *Cryptophagus*. Joy (1932) retains three of the four as genera, but does not consider the position of *Mnionomus*, as no species were at that time known to occur in Britain. Kloet and Hincks (1945) list *Micrambinus bimaculatus* (Panzer) as a *Cryptophagus*, retaining only *Cryptophagus* and *Micrambe* as genera. However, both Reitter (1908-16) and Bruce (1936) consider *bimaculatus* (Panzer) to be a *Micrambe* and regard both *Micrambe* and *Mnionomus* as subgenera of *Cryptophagus*. From our study of the genitalia of the group we consider that this last treatment is correct and Mr. J. Balfour-Browne (*in litt.*) concurs.

The reliability of the various taxonomic characters.

Most authors who have studied this genus emphasise the high degree of variability found in most of its component species. During our work on *Cryptophagus* we made collections in warehouses, flour mills, farm grain-stores and similar places where the beetles were to be found in very large numbers. We have thus had the opportunity to examine very large numbers of certain species—for example, several thousand *saginitus* from a single granary, and about a thousand *pilosus* from one farm grain-store. As a result we have come to the conclusion that some species are even more variable than has previously been suggested. We have, therefore, abandoned almost entirely some of the characters which were widely used in keys by previous authors. Our own key

is based entirely upon external morphological features, but we must emphasise that, in many species, the only completely reliable characters are those provided by the male genitalia.

We consider below the reliability of the various external morphological characters. It is important to realise that, in this genus, some of the best features for use in a key are only apparently, and not measurably, different in the various species. Careful comparison with the figures is therefore as important as careful use of the key. The words "apparently" or "appearing" have been used throughout the key to designate such features. Where there are constant, measurable differences between species, and elsewhere when we have considered it advantageous, measurements have been given. A diagram (fig. 8) illustrates where these were made.

(1) *Size.*

The British species of *Cryptophagus* all fall within the range of length 1.5-3.8 mm. The smallest species, *scutellatus*, varies from 1.5-1.8 mm. and the largest, *populi*, from about 2.8-3.8 mm. Nearly all other species vary over most of the intervening size range. For example, in a collection of about 100 *saginitus* (which is not one of the most variable species) from a farm grain-store about 10 per cent. measured approximately 1.8 mm., a similar proportion about 2.6 mm., and the remainder were intermediate. Thus only *scutellatus* and *populi* are separable from all other species on the basis of size, and we have used this feature in the key only in conjunction with other characters.

(2) *Colour.*

The presence or absence of a characteristic colour pattern is often a very useful guide to the identity of a specimen. It must not, however, be relied upon for this purpose, for not only do such colours sometimes disappear soon after death, but a small proportion of unicolorous individuals occurs in most normally bicoloured species. Also, some normally unicolorous species may form colour races in certain localities or habitats. For example, we have made collections of *saginitus* in which every individual, normally unicolorous red-brown, possessed an almost black pronotum, and other examples could be quoted. An extreme case was a specimen of *distinguendus*, which possessed the colour pattern of the typical form of *obsoletus*. *C. distinguendus* is normally unicolorous red-brown, or with only the pronotum black (*umbratus* Erichson), but closely resembles *obsoletus* in several other respects.

(3) *Proportional lengths of pronotum and elytra.*

This feature has sometimes been used to separate species. For example, in his description of *lapponicus* Gyllenhal Bruce states that the elytra are almost four times as long as the pronotum. In his key Hinton (1945) unfortunately bases his separation of *lapponicus* upon this statement. However, measurement of Bruce's photograph of *C. lapponicus* reveals that the elytra are less than three times as long as the pronotum, and our measurements of a number of British specimens, and of two examples supplied by Bruce, confirm the accuracy of the photograph. Moreover, although many species appear to differ appreciably in this respect, measurement indicates that in all species the

length of the elytra is approximately three times that of the pronotum, and that this ratio varies within a species as much as between species. This feature has therefore not been used in the key.

(4) *Head.*

(a) *Antennae.*—In a few instances antennal characters, particularly the structure of the club and the robustness of the funiculus, are of value and, when present, seem to be constant.

(b) *Eyes.*—The size and shape of the eyes, and the size of the individual facets, varies from species to species. Unfortunately the facet size is not easy to estimate, as the position of the insect during examination and the lighting used are critical factors. The apparent size of the punctures of the head or pronotum is also greatly influenced by these factors, and for this reason we are unable to follow Hinton (1945) in estimating the size of one by comparison with the other. Consequently small differences in eye characters are unreliable, but in several species they are of sufficient magnitude to be readily appreciated, and are then used in the key.

(5) *Pronotum.*

In *Cryptophagus* the form of the pronotum as a whole is the most important single external feature by which species may be recognised. This characteristic general appearance may, of course, be analysed by studying individual pronotal features, but few of these characters are constant and most are less convincing when examined separately than when assessed by their combined influence upon the general form of the pronotum. For this reason the whole pronotum and elytral base of each species has been illustrated.

(a) *Proportions of pronotum.*—The “nearly quadrate” as opposed to “distinctly transverse” pronotum has been widely used in most keys to *Cryptophagus*. It is indeed a useful character, but it is the apparent and not the measured proportions which are of greatest value. When large numbers of individuals are measured it becomes obvious that very few species are clearly separable on this basis. The apparent shape depends not only upon the measurable proportions of the pronotum, but upon the shape of the sides, the prominence of the callosity and the width of the base of the elytra. In the key two major separations are based upon this character and an approximate ratio of length to breadth is given as a general guide. This measurement is moderately reliable because borderline species have been taken both ways, but it is probable that a few individuals of most of the species concerned will fall outside the given range.

(b) *Structure of callosity.*—The pronotal callosities are formed by a thickening of the anterior angles of the pronotum and are a characteristic of the genus. They provide several of the most valuable characters and also determine to a considerable extent the general appearance of the pronotum. Since many of the features of the callosity are variable, their value depends upon precise definition and this is provided in a later section.

(c) *Position of lateral tooth.*—The position of the lateral tooth relative to the middle of the lateral margin of the pronotum has, in the past, been widely used to separate the species of *Cryptophagus* into smaller groups. Both of Bruce's

keys depend to a considerable extent upon this feature, which is, however, one of the least reliable of those normally used for major group separations. Measurement of numbers of specimens shows that, of all the British species, only *scutellatus* has the lateral tooth clearly and constantly in front of the middle of the pronotal side and only that of *obsoletus* is equally obviously behind middle. In all other species variation covers at least two possible positions—i.e. at or in front of middle; at or about middle; and at or behind middle—although in many species there is a definite tendency to vary in one direction from the mid-point. Also, as was the case with the degree of transversity of the pronotum, the lateral tooth in a given species may consistently appear in front of middle even though precise measurement fails to confirm the constancy of this feature. We have, therefore, used position of lateral tooth in the key on a number of occasions, but only in conjunction with other characters and never as the basis of a major group separation.

(d) *Shape of the pronotal sides.*—While it is often easy to distinguish sides that are rounded evenly from callosity to posterior angle from those that are angled at the lateral tooth, there is no clear-cut distinction between the two types, and it is sometimes difficult to assign a particular specimen to one or other of these categories with any confidence. We have taken care, in the key, to describe the feature in some detail, as it has a considerable influence upon the general appearance of the pronotum.

(e) *Punctuation.*—The pronotal punctuation may be compared with that of the elytra of the same specimen as regards strength and density or a comparison may be made between the pronotal or elytral punctuation of two individuals. Neither of these comparisons forms a very reliable criterion upon which to base a determination. In many species the punctuation is highly variable—e.g. in *pilosus* Gyllenhal it varies from strong to fine and from dense to diffuse. Also, even where constant differences exist, the condition and position of the insect and, particularly, the lighting used during examination, greatly influence the apparent size and density of the punctures. The combination of these conditions used at any one examination cannot be exactly reproduced with different apparatus. We have, therefore, relied as little as possible upon punctuation differences unless these are sufficiently distinct and constant to be readily appreciated. (See "Explanation of terms" for details of method of examination).

(f) *Basal foveae, furrow and fold.*—On each side of the pronotum at the base, there is a small pit—the basal fovea—which is connected to its fellow by a slight depression—the basal furrow. This furrow is sometimes traversed in the mid-line by a ridge—the basal fold. In the older keys the presence or absence, or the degree of development, of some or all of these features was often used to separate species or groups of species. We found that these features were so ill-defined and variable as to be virtually useless, and would, in any case, have been of value only where satisfactory separations could be made on better characters.

(6) *Elytra.*

The general shape of the elytra is occasionally sufficiently distinct to distinguish a species and is often of value as a confirmatory character.

(a) *Pubescence*.—A primary separation of species into two groups, based upon the possession of single or double pubescence (see "Explanation of terms") is a feature of most keys. Occasionally, however, both types occur in a single species. Apart from these two main types, which are usually fairly readily distinguished, the minor differences in pubescence which have often been used in the past are highly variable, and of little value as taxonomic characters.

(b) *Puncturation*.—This has already been considered under heading 5 (e) above. It should, however, be emphasised that elytral puncturation becomes progressively finer and more diffuse from base to apex, and should always be studied near the base as shown in fig. 7c. We have not found the puncturation gradient from base to apex of the elytra to be of any taxonomic value, although it has, in the past, been used to separate certain species.

The male genitalia.

Bruce (*op. cit.*) gives a brief description of the male genitalia. He refers to the parameres as distinct from, rather than part of, the aedeagus, the latter consisting of "apicalteil" (= aedeagus of Snodgrass (1935)), "basalteil" (= aedeagal apodeme of Snodgrass) and preputial sac (so named by both authors). We use the terminology of Snodgrass throughout, and include one structure not figured or named by Bruce—the sac which lies ventral to the apodeme which we identify with the endophallus of Snodgrass. This frequently shows spicules and other, feather-like structures which are occasionally of value as confirmatory taxonomic characters.

We give a diagram of the male genitalia of *pallidus* Sturm (fig. 127) in which are shown all the structures which we have found to be of value taxonomically. Many of these structures are present in all species but are much more conspicuous in some than in others, and may be absent altogether. Also, their appearance may vary in different individuals. Our figures of the aedeagi are therefore intended to give only a general impression, and detailed structural comparison should not be made except in respect of features mentioned under the appropriate heading in the notes on the species. The parameres are very much more constant in appearance than the aedeagi when prepared by the method described below, and our drawings represent fairly accurately the structures present. The number of setae, etc., is not completely constant within a species, but the general frequency of pores and setae, and their distribution, is fairly constant. In general, most reliance should be placed upon paramere structure, as there are few distinct and constant features in the aedeagus.

We have followed Bruce (*op. cit.*) to a considerable extent as regards technique of preparation, but have simplified his procedure to some extent.

Our method is as follows:

Soften the specimen by brief immersion (up to half minute) in boiling water.

Remove the abdomen by inserting a fine needle between the metasternum and the first abdominal segment.

Boil the abdomen in 10 per cent. caustic potash solution for one to two minutes. Allow to stand in hot solution for about ten minutes.

Slit open the soft dorsal surface of the abdomen under water, and dissect out the male genitalia. Remove the apical plate—a small chitinous spicule which frequently remains attached to the parameres.

Mount in Swan's Fluid (Swan, 1936), bringing the mount to the boil over a Bunsen flame. For a permanent preparation seal the edges of the coverslip with varnish or wax.

It should be noted that males of *Cryptophagus* (except *C. abietis*) possess four-segmented hind tarsi, as opposed to the five-segmented tarsi of the females.

II. EXPLANATION OF TERMS USED IN THE KEYS.

Colour : Reliable only with fresh examples as colour changes sometimes occur in old specimens.

Pronotum : *Width* is measured across the widest part (usually the level of the lateral teeth), excluding lateral teeth.

Length is measured parallel to the median axis from the anterior limit of the callosity (see below) to the line joining the posterior angles (fig. 8, 3A-3D).

Callosity :

Size.—refers to length in relation to length of pronotum (fig. 8, 4A-4B/4A-4D). When callosity does not project anteriorly its anterior limit is taken as the point of intersection of its margin with the anterior margin of the pronotum. Its posterior limit is defined by the apex of the posterior angle or the tip of the tooth.

Prominence.—Refers to the degree to which the callosity stands out laterally from the sides of the pronotum.

Upturning.—Refers to the extent to which the face of the callosity is visible when viewed from above.

Dorsal rim.—Refers to the upstanding edge of the face of the callosity. It is described as "strong" when it forms a vertical, plate-like lamina, and as "weak" when it forms only a low, rounded ridge.

Anterior projection.—Refers to the extent to which the anterior point of the callosity projects beyond the anterior margin of the pronotum. In the key the feature is used only in cases where this projection is marked.

Hook-tooth (fig. 2d) is formed when the posterior angle of a callosity with a weak dorsal rim is drawn out into a fine point.

Rim-tooth (fig. 2f) is formed when a callosity with a strong dorsal rim, which projects posteriorly, is viewed from above in the plane of the face. The rim, then seen in profile, appears as a tooth-like projection.

Sides :

Angled or rounded.—These features are best appreciated under a low magnification.

Elytra :

Pubescence (Fig. 1) :

This should be studied on the disc of the elytra because some species with single pubescence have longer, more or less raised hairs at the sides. In species possessing double pubescence the longer, erect

hairs are very conspicuous; in *cellaris* the rows of long but semi-decumbent hairs are best seen with light coming from in front of the insect.

Puncturation (Figs. 9-48): The drawings were made from specimens illuminated by light transmitted along a perspex rod, one end of which had a "ground-glass" finish. The areas chosen for drawing were squares of 0.1 mm. side in the positions shown in fig. 7c.

Density.—Comparison of average distance between the rims of adjacent punctures with average diameter of punctures.

Strength.—The average size of punctures (usually as a comparison between pronotum and elytra, or a direct comparison between species).

Genitalia: Some species can be determined with certainty only by a study of the male genitalia; these are indicated in the key by the letter (G).

III. KEY TO THE SUBGENERA OF *CRYPTOPHAGUS* (HERBST).

1. Pronotum with sides behind callosity bearing teeth throughout their length; antennae rather long and slender (except *bimaculatus*) . . . subgen. **Micrambe** Thomson
- Pronotum with sides behind callosity bearing only one tooth; antennae rather shorter and more robust (except *acutangulus*) . . . 2
2. Membranous wings present . . . subgen. **Cryptophagus** s. str.
- Membranous wings reduced or absent . . . subgen. **Mnionomus** Wollaston

For convenience, *C. simplex* Miller, the only British species of *Mnionomus*, is included in the key to *Cryptophagus* s.str.

IV. KEY TO THE SPECIES OF *CRYPTOPHAGUS* S.STR. AND *MNIONOMUS* WOLLASTON.

1. Pubescence decumbent with longer sub-erect hairs (fig. 1a) or with longer obliquely raised hairs in rows resembling striae (fig. 1c) . . . 2
- Pubescence entirely decumbent, except at the sides, with hairs of approximately equal length (fig. 1b) . . . 9
2. Callosity with a hook-tooth, without or with a very weak dorsal rim (fig. 2d) . . . 3
- Callosity right-angled or obtuse-angled behind, with (figs. 2e, 2f) or without (figs. 2a, 2b, 2c) a rim-tooth . . . 5
3. Apex of anterior tibia produced externally into a strong tooth (fig. 6b). (Pubescence very long and coarse; antennae robust) . . . **lycoperdi** Scopoli (p. 250)
- Anterior tibia without a strong too that apex. (Pubescence finer and shorter) . . . 4
4. Species black, shoulders of elytra obscurely reddish. Sides of pronotum not angled at lateral tooth but appearing rather parallel-sided with a gradual sinuation along length (pronotum narrower than base of elytra) . . . **ruficornis** Stephens (p. 250)
- Species unicolorous reddish. Pronotum with sides usually angled at tooth and converging from tooth to base . . . **pilosus** Gyllenhal (p. 251)
5. Pronotal puncturation very fine and diffuse, many of the punctures being separated by more than one diameter; elytral puncturation similar to, or slightly stronger and denser than, that of the pro-

- notum. (Callosity very weakly thickened, with a very weak dorsal rim, hardly defined posteriorly but projecting anteriorly beyond the margin of the pronotum; pronotum appearing quadrate, sides evenly rounded, lateral tooth very small. Elytra narrow, sides strongly rounded, pubescence sparse. Membranous wings reduced or absent) **simplex** Miller (p. 250)
- Pronotal puncturation never very fine and diffuse, very few punctures separated by as much as one diameter; elytral puncturation always more diffuse and usually finer than that of pronotum. Membranous wings present 6
6. Eyes large, with large facets (fig. 4c). (Elytral pubescence with the longer hairs obliquely raised, and arranged in rows resembling striae (fig. 1c). Elytra usually long, narrow and parallel-sided) **cellaris** Scopoli (p. 250)
- Eyes not large. (Elytral pubescence with longer hairs sub-erect, not resembling striae) (fig. 1a) 7
7. Eyes small and conical (fig. 4a) **laticollis** Lucas (p. 250)
- Eyes of normal size, hemispherical 8
8. Callosity with a strong dorsal rim. Elytral puncturation nearly as strong and dense as that of pronotum. Elytra broadly oval **setulosus** Sturm (p. 251)
- Callosity with a weak dorsal rim. Elytral puncturation finer and more diffuse than that of pronotum. Elytra long, tapering, with sides strongly rounded **schmidtii** Sturm (p. 251)
9. Callosity very strongly produced laterally. (Lateral tooth usually very large, at or somewhat behind middle of side. Eyes very large and prominent with large facets (fig. 4c) **acutangulus** Gyllenhal (p. 251)
- Callosity not very strongly produced laterally 10
10. Callosity with a hook-tooth (without or with a very weak dorsal rim) (fig. 2d) 11
- Callosity right-angled or obtuse-angled behind, with (figs. 2e, 2f) or without (figs. 2a, 2b, 2c) a rim-tooth 14
11. Lateral tooth in front of middle of side. Pronotum only slightly transverse, with sides usually lightly and evenly rounded; punctures often separated by as much as one diameter; callosity moderately large (one-fifth to one-sixth of side) **labilis** Erichson (p. 251)
- Lateral tooth at or behind middle of side 12
12. Pronotum appearing parallel-sided; lateral tooth behind middle of side; callosity projecting strongly beyond anterior margin of pronotum. (Pronotal puncturation stronger and denser than that of elytra; elytra usually pitchy black with two reddish marks on the shoulders and near the apices; occasionally unicolorous reddish. Length 2.2-2.8 mm.) **obsoletus** Reitter (p. 251)
- Pronotum not appearing parallel-sided; lateral tooth at or slightly behind middle of side; callosity not, or only slightly, projecting beyond the anterior margin of the pronotum (species usually unicolorous, or with pronotum darker than elytra) 13
13. Species small (length 1.6-2.2 mm.). Callosity small (less than one-sixth of side); lateral tooth often slightly behind middle of side. (Sides seldom strongly angled but often appearing sinuate, i.e. slightly concave in front of lateral tooth and slightly convex behind; pronotal puncturation rather fine and moderately diffuse) (G) **distinguendus** Sturm (p. 252)

- Species moderately large (length 2.0–3.2 mm.). Callosity moderately large (more than one-sixth of side); lateral tooth usually at middle of side. (Sides often strongly angled at lateral tooth, sometimes evenly rounded but never sinuate) **pilosus** Gyllenhal (p. 252)
- 14. Pronotum much narrower than the enlarged, convex elytra (fig. 3a). (Pronotum parallel-sided, appearing almost quadrate; lateral tooth very small, at or slightly behind middle of side) **fallax** Balfour-Browne (p. 253)
- Pronotum as wide as, or only slightly narrower than, elytra; elytra not enlarged (fig. 3b) 15
- 15. Species large (length 3.2–3.8 mm.). Club of antenna only slightly broader than the robust funiculus (fig. 5c). (Anterior tibia toothed externally at apex (fig. 6b)) **populi** Paykull (p. 253)
- Species smaller (length less than 3.0 mm.). Club of antenna about twice as broad as funiculus (figs. 5a, 5b) 16
- 16. Basal segment of antennal club much narrower than second segment (fig. 5b) 17
- Basal segment of antennal club as wide, or almost as wide, as second segment (fig. 5a) 18
- 17. Sides of pronotum straight, diverging from callosity to near base, converging abruptly close to base (fig. 23), but sometimes slightly and evenly rounded from tooth to base (fig. 24). (Callosity slightly smaller. Antennal club usually with apical segment enlarged and basal segment very small. Species unicolorous reddish) **pubescens** Sturm (p. 254)
- Sides of pronotum hardly divergent, always strongly rounded from tooth to base. (Callosity slightly larger. Antennal club with apical segment normal, basal segment usually only slightly reduced in size. Species with pronotum and shoulders of elytra reddish, remainder of elytra pitchy black) **micaceus** Rey (p. 254)
- 18. Species small (length 1.5–1.8 mm.). (Callosity small, about or less than one-seventh of side; pronotal puncturation very fine and diffuse; lateral tooth well in front of middle of side) **scutellatus** Newman (p. 254)
- Species larger (length more than 2.0 mm.) 19
- 19. Face of callosity not standing out from the lateral margin of the pronotum, but running into it posteriorly at an obtuse angle (callosity not, or only slightly, prominent laterally (e.g. figs. 28, 29, 30)) 20
- Face of callosity standing out from the lateral margin of the pronotum, joining it posteriorly at a distinct angle (e.g. figs. 31, 32, 39, 40) 26
- 20. Sides of pronotum strongly angled at lateral tooth (e.g. figs. 32, 37, 38, 42), sometimes, in addition, concave between callosity and tooth (e.g. fig. 42) and usually converging from tooth to base in an almost straight line 21
- Sides of pronotum not, or only very slightly, angled at lateral tooth, usually more or less evenly rounded from callosity to base (e.g. figs. 28, 29, 30) 22
- 21. Face of callosity strongly upturned. (Species usually bicoloured, with pronotum and shoulders of elytra reddish and remainder of elytra dark; sometimes unicolorous reddish. Elytra short, oval; pronotum distinctly transverse (more than 8:5); lateral tooth at or about middle of side) G. **scanicus** L. (p. 261)
- Face of callosity not, or only slightly, upturned. (Species with elytra always unicolorous reddish, often rather long and parallel-

- sided; pronotum appearing only slightly transverse (less than 8 : 5); lateral tooth sometimes near, but often distinctly in front of, middle of side) **dentatus** group (p. 256)
22. Pronotum appearing somewhat flattened. Elytral puncturation almost as strong and dense as that of pronotum **subdepressus** Gyllenhal (p. 255)
- Pronotum normally convex. Elytral puncturation finer and more diffuse than that of pronotum 23
23. Callosity with strong dorsal rim 24
- Callosity with weak dorsal rim 25
24. Pronotum appearing only slightly transverse (less than 8 : 5); callosity smaller (about one-fifth of side), sometimes projecting slightly beyond anterior margin of pronotum. (Lateral tooth usually in front of middle of side) **dentatus** group (p. 256)
- Pronotum appearing distinctly transverse (more than 8 : 5); callosity larger (about one-fourth of side), and projecting strongly beyond anterior margin of pronotum. (Position of lateral tooth very variable) **subfumatus** Kraatz (p. 255)
25. Lateral tooth in front of middle of side; pronotal puncturation rather diffuse. (Pronotum appearing only somewhat transverse (less than or about 8 : 5). Elytra short oval, tapering strongly to apex) **saginitus** Sturm (p. 254)
- Lateral tooth behind middle of side, very small; pronotal puncturation dense. (Pronotum appearing distinctly transverse (about or more than 9 : 5). Elytra broad, not strongly tapering) **lapponicus** Gyllenhal (p. 255)
26. Pronotum appearing only slightly transverse (less than 8 : 5) (e.g. figs. 31-35) 27
- Pronotum appearing distinctly transverse (more than 8 : 5) (e.g. figs. 37, 38) 30
27. Lateral tooth usually slightly behind middle of side. Species long and narrow, appearing almost cylindrical (fig. 7a) **angustus** Ganglbauer (p. 255)
- Lateral tooth at or in front of middle of side. Species not appearing cylindrical (e.g. figs. 7b, 7c) 28
28. Callosity small or moderate in size (usually about or less than one-fifth of side, very occasionally (some *intermedius*) about one-fourth), not, or only slightly upturned (e.g. figs. 32-34) 29
- Callosity large (about one-fourth of side), strongly upturned (e.g. figs. 39-42) 34
29. Puncturation of pronotum much stronger than that of elytra (except *intermedius*). (Lateral tooth usually in front of middle of side; callosity without, or with a very small, rim-tooth; pronotum normally convex, sides variable but rarely sinuate) **dentatus** group (p. 256)
- Puncturation of pronotum only somewhat stronger than that of elytra. (Lateral tooth at or about middle of side; callosity usually with a strong rim-tooth; pronotum somewhat flattened, its sides strongly rounded behind lateral tooth, sometimes sinuate between callosity and base) (G) **corticinus** Thomson (p. 259)
30. Species very densely punctured, elytral puncturation almost as strong and dense as that of pronotum. (Pronotum somewhat depressed) **subdepressus** Gyllenhal (p. 255)
- Elytral puncturation finer and more diffuse than that of pronotum 31
31. Callosity small (less than one-sixth of side). (Lateral tooth in front of middle of side; sides converging strongly from lateral tooth to base in an almost straight line) **subvittatus** Reitter (p. 260)

- Callosity larger (about or more than one-fifth of side) 32
- 32. Callosity moderately large (about one-fifth of side), face not, or only very slightly upturned (figs. 36, 38). (Elytra rather long and parallel-sided) 33
- Callosity large (about or more than one-fourth of side), rather strongly upturned (figs. 39-42) 34
- 33. Pronotum somewhat flattened, its sides strongly rounded from lateral tooth to base, not angled at tooth, sometimes sinuate between callosity and base **corticinus** Thomson (p. 259)
- Pronotum normally convex, its sides angled at lateral tooth, usually concave between callosity and tooth, converging from tooth to base in an almost straight line. (Elytra characteristically lighter than pronotum, often pale yellow) **hexagonalis** Tournier (p. 260)
- 34. Anterior margin of pronotum strongly sinuate where it runs into anterior margin of callosity; callosity upturned, with a strong dorsal rim; side usually concave between callosity and lateral tooth, usually angled at tooth, and converging from tooth to base in an almost straight line; puncturation of pronotum usually strong and dense (G) **postpositus** Sahlberg (p. 260)
- Anterior margin of pronotum very slightly sinuate where it runs into anterior margin of callosity; callosity upturned, with a moderately strong dorsal rim; side often concave between callosity and lateral tooth, slightly angled at tooth, or evenly rounded behind tooth; puncturation of pronotum rather diffuse to moderately dense (G) **badius** Sturm (p. 260)
- Anterior margin of pronotum sometimes slightly sinuate but often flattening only slightly where it runs into anterior margin of callosity; callosity usually somewhat upturned, with a strong dorsal rim; side evenly rounded, not concave between callosity and lateral tooth, not angled at tooth; pronotal puncturation variable but always strong and usually dense (G) **pallidus** Sturm (p. 261)
- Anterior margin of pronotum flattening only slightly where it runs into anterior margin of callosity; callosity usually strongly upturned, often with weak dorsal rim; side often concave between callosity and lateral tooth, usually angled to some extent at tooth; puncturation of pronotum strong and usually moderately dense, that of elytra sometimes very fine. (Typically with pronotum and shoulders of elytra light reddish and remainder of elytra dark brown, but occasionally unicolorous reddish (G)) **scanicus** L. (p. 261)

V. KEY TO THE SPECIES OF *MICRAMBE* THOMSON.

- 1. Pubescence decumbent with longer sub-erect hairs (fig. 1a) 2
- Pubescence entirely decumbent, except at the sides, with hairs of approximately equal length (fig. 1b) 3
- 2. Eyes prominent, conical, with large facets (G) **lindbergorum** Bruce (p. 263)
- Eyes prominent and with large facets, but spherical (G) **villosus** Heer (some *vini*) (p. 262)
- 3. Face of callosity standing out from the lateral pronotal margin so that the pronotum is much wider across the posterior angles of the callosities than across the sides immediately behind them **vini** Panzer (p. 262)
- Face of callosity more or less in line with the lateral pronotal margin so that the pronotum is very little wider across the posterior angle of the callosities than across the sides immediately behind them 4

4. Callosity smaller (about one-sixth of side), not upturned. (Sides of pronotum very evenly rounded; elytra strongly rounded and convex, with a dark patch on the middle third of each) *bimaculatus* Panzer (p. 261)
- Callosity larger (about or more than one-fourth of side), usually somewhat upturned. 5
5. Pronotum moderately strongly and rather diffusely punctured. (Pronotal sides converging somewhat towards base) *aubrooki* Donisthorpe (p. 263)
- Pronotum finely and very densely punctured. (Pronotal sides converging only slightly towards base). Hind tarsi of male five-segmented *abietis* Paykull (p. 262)

VI. NOTES ON THE SPECIES OF *CRYPTOPHAGUS* S.STR. AND *MNIONOMUS* WOLLASTON.

The information given in these notes has been arranged under three headings for each species.

(1) *General and comparative notes.*

Under this heading we deal with any general taxonomic points which require detailed explanation; indicate the most closely related species or those with which confusion is most likely; and give, where possible, the range of variation, emphasising any particularly reliable features, or additional points not mentioned in the key.

(2) *Male genitalia.*

The structure of the parameres as illustrated by our figures is usually sufficiently distinct to distinguish a species from its allies. Therefore, points of difference are given only when the figures are inadequate or the differences small. When good aedeagal characters occur they are mentioned under this heading, and features not so mentioned should not be relied upon. Thus, when no comments are made under this heading, it is to be assumed that the parameres, as figured, are characteristic, and that the aedeagus shows no good features.

(3) *Habitat.*

Certain species of *Cryptophagus* are usually associated with particular habitats but there are certain general habitats in which many species occur. We give below the results of our own observations, made in Britain, for three of these general habitats. Others include vegetable refuse, fungi, and nests of rodents, bees and wasps.

(a) In buildings (warehouses, farms, houses, etc.) Very commonly—*cellaris distinguendus*, *pilosus*, *saginatus*, *scutellatus*, *subfumatus*. The first of these was only very rarely, and the last never, found in the open.

Occasionally—*acutangulus*, *dentatus*, *laticollis*, *obsoletus*, *postpositus*, *pseudodentatus*, *rotundatus*, *scanicus*, *simplex*.

Rarely—*fallax*, *hexagonalis*, *populi*, *subvittatus*.

(b) In haystacks—*acutangulus*, *distinguendus*, *laticollis*, *pallidus*, *pilosus*, *pseudodentatus*, *saginatus*, *scutellatus*.

(c) In birds' nests (see Woodroffe, 1953b)—*acutangulus*, *cellaris*, *distinguendus*, *pallidus*, *postpositus*, *saginat*, *scanicus*, *scutellatus*, *subfumatus*.

Where, in our experience, or according to Hinton (1945), a species occurs frequently in one of these habitats, the simple entry "general" is made.

Where a species is widely known to prefer a particular habitat, according to many authors, the habitat is quoted without authority. In other cases the source of the information is given, but, except for those of Bruce, such records should not be accepted as entirely reliable. All references to Bruce are to be found in Bruce (1936) and to Hinton in his monograph (1945).

Throughout these notes synonymy is given only when the alternative names are still widely used or where recent changes have been made. When no authority is given details will be found in either Bruce or Hinton.

C. lycoperdi Scopoli. (Figs. 9, 6 (b) ; ♂ Figs. 51, 94.)

In general facies resembling the form of *pilosus* which has double pubescence, and in the robust antennae and toothed tibiae close to *populi*.

Male genitalia.—The parameres are fairly characteristic and all our preparations differ considerably from Bruce's figure for this species.

Habitat.—Usually found in fungi.

C. ruficornis Stephens (= *nigritulus* Reitter ; see Bruce, 1942).

(Fig. 10 ; ♂ Figs. 52, 95.)

Rather similar to *pilosus*, but the slightly sinuate sides of the pronotum are very characteristic.

Male genitalia.—The aedeagus is very distinct from that of *pilosus*, being similar to that of the *dentatus* group.

Habitat.—Usually occurs in fungi.

C. simplex Miller (subgen. *Mnionomus*). (Fig. 12 ; ♂ Figs. 54, 97.)

The only British representative of the subgenus, this species is quite unlike any other British *Cryptophagus*. The pronotum possesses no basal foveae.

Habitat.—In this country it occurs only in granaries, flour mills, etc. (Coombs and Woodroffe, 1952a, b). Bruce, quoting Reitter and Ganglbauer, gives fungi, and states that the species is extremely rare.

C. cellaris (Scopoli). (Figs. 13, 1 (c), 4 (c) ; ♂ Figs. 55, 98.)

In shape usually rather similar to *dentatus*—i.e. long and parallel-sided. The typical pubescence is not always easy to detect, but the large eyes with large facets will readily distinguish the species from *dentatus*. The fine, somewhat diffuse and very even pronotal puncturation is also rather characteristic.

Habitat.—General, but almost invariably indoors. One of the commonest warehouse species.

C. laticollis Lucas (= *affinis* Sturm). (Figs. 14, 4 (a) ; ♂ Figs. 56, 99.)

Externally this species resembles *setulosus*, but is usually smaller. The pronotum is rather variable in shape, some examples resembling *setulosus* more closely than others. The pubescence is usually conspicuously double, but in

occasional examples it may rather resemble that of *cellaris*. The eye character is particularly useful.

Habitat.—General, but seldom in any numbers. Bruce considers this species to be much less common than the records suggest.

C. setulosus Sturm. (Fig. 15 ; ♂ Figs. 57, 100.)

This species is quite distinct from all others except *schmidtii* and some specimens of *laticollis*. It is not a very variable species and is readily separable from its allies on the characters given in the key. The strong and dense elytral puncturation is conspicuous.

Male genitalia.—The parameres rather resemble those of *schmidtii*, but are more strongly tapering and have pronounced, as opposed to slight, basal emarginations. The structure of the aedeagus is unique, only that of *corticinus* bearing any resemblance to it.

Habitat.—Associated with bees' nests. Hinton gives one record from a granary.

C. schmidtii Sturm. (Fig. 16 ; ♂ Figs. 58, 101.)

Closely related to the previous species, but generally readily separable from it. The strongly tapering elytra are a most useful feature, which seems to be constant, though we have examined few specimens.

Male genitalia.—The parameres are close to those of *setulosus*, but the sides are more rounded and the basal emargination is shallow. In contrast to that of *setulosus*, the aedeagus shows no conspicuous features.

Habitat.—We have never found this species. According to Bruce it inhabits marmots' nests and Hinton gives granaries and a haystack.

C. acutangulus Gyllenhal. (Figs. 17, 4 (c) ; ♂ Figs. 59, 102.)

This very distinct species should not be confused with any other, but, in some respects, resembles *cellaris*, particularly in the large, coarsely-faceted eyes and the long, rather parallel-sided elytra.

Habitat.—General.

C. labilis Erichson. (Fig. 18 ; ♂ Figs. 60, 103.)

Although it has hitherto remained unrecognised in Britain, this species should not be confused with any other. It is probably closest to *intermedius*.

Male genitalia.—The parameres are similar to those of *angustus* and the aedeagus is of the *dentatus* type.

Habitat.—We have discovered this species twice only—from Moccas Park, Hereford (coll. G. H. Ashe) and Cambridge (University Museum coll.) labelled "Trinity Fellow's Garden, under bark". Bruce gives under bark and in rotten wood as the habitat.

C. obsoletus Reitter. (Fig. 22 ; ♂ Figs. 62, 105.)

In spite of its very distinct appearance we have had considerable difficulty in finding constant characters upon which to separate this species from *distinguendus*. The typical coloration of *obsoletus* is often a useful guide, and, in spite of the apparent lack of distinguishing characters, the general form of

the pronotum is very characteristic. The tooth on the callosity is very small, though always distinct and we cannot understand Bruce's failure to discern this feature, nor his estimate of the position of the lateral tooth as in the middle of the pronotal side when it is so clearly and constantly behind middle. The brief description of this species given in Coombs and Woodroffe (1952a) requires modification as our estimate of callosity size was based on different measurements from those we now use. The callosity is usually larger than that of *distinguendus*, frequently attaining one-fifth of the pronotal side, but varying down to one-seventh of side. It projects anteriorly in a very characteristic manner.

Male genitalia.—The aedeagus is expanded apically, forming a footlike projection on each side, and is thus distinguishable from any other British species of *Cryptophagus* s. str.

Habitat.—In this country it has been found indoors only, in granaries, flour mills, etc. (Coombs and Woodroffe 1952a, b.) Bruce describes it as a rare East Siberian species, but gives no information as to habitat.

C. distinguendus Sturm (= *umbratus* Erichson = *stramenti* Donisthorpe). (Fig. 19; ♂ Figs. 61, 104).

The close similarity between *distinguendus* and *obsoletus* has already been dealt with. The only other possible confusion is with the form of *pilosus* which possesses single pubescence, and it is often extremely difficult to separate certain individuals of *distinguendus* from extreme examples of this form of *pilosus*. The rather fine and moderately diffuse pronotal puncturation of *distinguendus* is often useful, but the puncturation of *pilosus* is so variable that no reliable separation can be based on this feature. The differences given in the key will separate the majority of specimens, but a certain amount of confusion between extreme forms is inevitable, and these can be determined with certainty only by a study of the male genitalia. It is, perhaps, worth noting that *pilosus* is probably the most highly variable of all the European species, and almost all specimens which we were unable to determine with certainty as either *distinguendus* or *pilosus* proved to be the latter when the genitalia were examined.

Male genitalia.—The aedeagus possesses few well-marked features, but the blunt apex, caused by the abrupt inward deflection, on each side, of the acuminate tip, is rather characteristic.

Habitat.—General.

C. pilosus Gyllenhal (= *punctipennis* Brisout). (Fig. 11; ♂ Figs. 53, 96.)

As has been stated above, under *distinguendus*, *pilosus* is an extremely variable species. Not only are all gradations in pubescence from single ("short-haired") to double ("long-haired") known, but the extreme forms, which are much commoner than intermediate types, may often be found living together. Also the shape of the elytra varies from short-oval to elongate, with sides only slightly rounded. The pronotal sides are usually angled at the lateral tooth, but in an appreciable number of individuals they appear to be evenly rounded. The pronotal puncturation varies from strong to fine and from dense to diffuse. The size of the callosity and the position of the lateral tooth also vary, but not more so than in other species. The separation of the "short-haired" *pilosus*

from *distinguendus* has already been dealt with under the latter species. Confusion with *labilis* is also possible, although specimens of *pilosus* combining evenly rounded pronotal sides with a lateral tooth in front of middle and diffuse pronotal puncturation are fortunately rare. The moderately large eye facets of such specimens will assist in separating them from *labilis*, which has fine facets. The confusion of "short-haired" *pilosus* with *badius* is considered under that species. The "long-haired" *pilosus*, which includes *punctipennis* Brisout, is closest to *lycoperdi* and *ruficornis*, but the separation of these species presents no difficulty.

Habitat.—General. One of the commonest species.

C. fallax Balfour-Browne (= *fumatus* auctt. nec Marsham; see Balfour-Browne, 1953). (Figs. 21, 3 (a); ♂ Figs. 63, 106.)

With its apparently almost quadrate thorax and inflated elytra, this species, in its typical form, is quite unlike any other. Occasional specimens of the *dentatus* group—especially *acuminatus*—approach this shape, and in fig. 3 a typical *fallax* is compared with an extreme example of *acuminatus*.

Bruce draws attention to the close relationship between *fallax* (= *fumatus* auctt.), *badius* and *quercinus* Kr. He has found apparently intermediate forms between the three species, and having failed to discern any difference in male genitalia, expresses the opinion that they are probably forms of one species. Since both *fallax* and *badius* are excessively rare in Britain, and *quercinus* has not been recorded at all, we are not in a position to say with complete certainty whether British material supports this view. The few British examples of *fallax* and *badius* which we have studied are quite distinct externally. Moreover, we cannot agree that there are no differences between the species in the characters of the male genitalia. The parameres of all available British specimens of *badius* differ in shape from Bruce's figure for that species, being rather intermediate between his figure for *badius* and that for *fuscicornis* (see also under *badius*), and two specimens supplied by Bruce possessed similar parameres. In contrast, his figures of the parameres of *fallax* and *quercinus* agree with our preparations. Thus, as regards the shape of the parameres and the distribution of their setae, there are slight differences between *badius* on the one hand and *fallax* and *quercinus* on the other. In addition to this, the thickened, funnel-shaped structure which surrounds the endophallic pore is, in *badius*, small and situated within the aedeagus, but in both *fallax* and *quercinus* it is larger, and situated entirely beneath the apodeme. We suggest, therefore, that upon the basis of British material *badius* and *fallax* are distinct species, but that *fallax* and the non-British *quercinus* may be, as Bruce maintains, only forms of one species.

Habitat.—The only specimens we have captured were taken from a piece of old carpet in the disused wing of a large country house in Hertfordshire (Woodroffe, 1953a). We know of no other authentic British records for which details of capture are available. European records cover a wide variety of habitats.

C. populi Paykull. (Figs. 20, 5 (c), 6 (b); ♂ Figs. 64, 107.)

This is the largest European species, and size alone is a useful guide to its identity. Also, there is frequently a broad, dark, longitudinal streak on each

elytron. The rather robust antennae and the dentate anterior tibiae suggest affinity with *lycoepardi*.

Habitat.—Apparently associated in some way with bees, but Allen (1952) suggests old fruit trees. We have identified it once from a warehouse.

C. pubescens Sturm. (Figs. 23, 24, 5 (b); ♂ Figs. 82, 126.)

The shape of the pronotum and the structure of the antennal club will distinguish this species from all others except *micaceus*. From this species it may be separated by a number of features (see key and also Allen, 1954) of which the form of the pronotum, especially as regards the shape of the sides behind the lateral tooth, is the most constant. This varies somewhat towards the shape of *micaceus*, but the sides behind the lateral tooth are never as strongly or as evenly rounded. We figure the pronotum of a typical specimen of each species and also an example of *pubescens* showing the extreme of variation towards *micaceus* in pronotal shape (fig. 24).

Bruce maintains that *micaceus* is only a colour form of *pubescens*, whereas Allen (1954) considers them to be distinct. There is something to be said for both views, for it is seldom possible to define precisely the stage at which diverging forms become species, and the two are certainly very closely related. However, in view of the not inconsiderable differences in external morphology and the fairly distinct habitats, we tend to support Allen's view that the two should, in spite of their identical male genitalia, be regarded as distinct.

Male genitalia.—We can find no good differences between this species and *micaceus*.

Habitat.—*C. pubescens* is typically associated with ground-nesting wasps, but has occasionally been found in general habitats.

C. micaceus Rey. (Figs. 25, 5 (b); ♂ Figs. 82, 126.)

See above under *pubescens*. The colour pattern resembles that of typical *scanicus*, and confusion with that species sometimes occurs. The colours are unstable, and may disappear soon after death, the specimens becoming uniform brown.

Habitat.—Occurs almost exclusively in the nests of tree-living wasps, especially hornets (*Vespa crabro* L.).

C. scutellatus Newman (= *bicolor* Sturm). (Fig. 26; ♂ Figs. 65, 108.)

This is the smallest species of the genus. It is probably closest to *dislinguendus*, but is unlikely to be confused with that, or any other, species. The lateral tooth is clearly and constantly in front of the midpoint of the pronotal sides, and the very fine, diffuse pronotal puncturation is also a constant and obvious feature.

Habitat.—General.

C. saginatus Sturm. (Fig. 28; ♂ Figs. 73, 114.)

This species is probably closest to *subfumatus*, *subdepressus* and *lapponicus*, but is so distinct that it should not be confused with any except very atypical examples of these species.

Habitat.—This is one of the commonest indoor species, and is abundant also in general habitats in the open.

C. subdepressus Gyllenhal. (Fig. 27 ; ♂ Figs. 70, 115.)

C. subdepressus is very close to *lapponicus*, from which it differs in the more prominent callosities and more strongly punctured elytra.

Male genitalia.—The aedeagus proper is short, but of the *dentatus* type, with strongly developed granular triangles in the preputial sac. (See below under *dentatus* group).

Habitat.—Generally found associated with coniferous trees.

C. subfumatus Kraatz. (Fig. 29 ; ♂ Figs. 72, 116.)

This species generally resembles *lapponicus*, but can usually be separated by its more elongate, more parallel-sided elytra, and by the more strongly developed callosities which project anteriorly beyond the margin of the pronotum. It is, however, a very variable species, and some individuals approach very closely to *lapponicus*.

Male genitalia.—The parameres are quite unlike those of any other species except, possibly, the non-British *archangelicus* Sahl.

Habitat.—It occurs almost exclusively indoors. Bruce mentions that it has been found on a cactus in Mexico ; there appear to be no other records of its occurrence in the open. In Britain it is usually associated with stored dried fruit.

C. lapponicus Gyllenhal (= *validus* Kraatz). (Fig. 30 ; ♂ Figs. 83, 117.)

Hinton, in a footnote (p. 224) states that there are no reliable records of *C. lapponicus* in Britain. This has been our experience also, for all specimens of supposed *lapponicus* which we have examined have proved to be *subfumatus*. We have, however, found the species in two collections. Mr. P. Harwood's collection included a long series of *Cryptophagus* which were taken from a squirrel's drey at Aviemore, Inverness, and which were standing as *subfumatus*. This remarkable series consisted of about equal numbers of *badius* and *lapponicus*, and provided us with the first authentic British specimens of both species. In addition, in the Champion collection at the British Museum, the short series of *subdepressus* included one *lapponicus*, also from Aviemore.

This species is closely similar to *subdepressus* and *subfumatus*. We have pointed out earlier that Hinton's separation of this species (based on information given by Bruce) on a ratio of pronotal to elytral length of 1 : 4 does not hold, and that this ratio is usually 1 : 3. The species is, in fact, shortly and broadly oval in shape, resembling *pallidus* and *subdepressus* in this respect. We have never seen any individual of any species of *Cryptophagus* in which the elytral length approached four times the pronotal length.

Habitat.—As mentioned above, the only known British specimens were taken from a squirrel's drey. Bruce quotes three records from similar situations, so this is probably an important habitat. He gives, also, birds' nests and fungi.

C. angustus Ganglbauer (= *parallelus* Thomson nec Brisout).
(Figs. 35, 7a ; ♂ Figs. 77, 121.)

This species is another about which considerable confusion exists. It has not hitherto been recorded as British, but there are a number of British records of *cylindrus* Kiesw. (= *parallelus* Brisout nec Thomson). All specimens

standing as *cylindrus* which we have examined have proved to be *angustus*, and we have failed to find the true *cylindrus* in British collections.

C. angustus has some affinity with the *dentatus* group and is very close to *cylindrus*. The last-named is apparently not British, but the following separation, taken from Bruce's second key, is given to enable it to be recognised should it occur.

Callosities rather strongly thickened, usually with a distinct angle posteriorly; pronotal puncturation rather strong and dense; elytral puncturation as strong as that of the pronotum but more diffuse.	
Species larger, 2.0-2.1 mm.	<i>angustus</i>
Callosities weakly thickened, rim-like, often indistinctly angled posteriorly; pronotal puncturation only moderately strong and dense; elytral puncturation much finer and more diffuse than that of pronotum. Species smaller, 1.6-1.8 mm.	<i>cylindrus</i>

In addition the lateral tooth of *angustus* is usually slightly behind the mid-point of the pronotal side, whereas that of *cylindrus* is at middle. From certain specimens of the *dentatus* group species, *angustus* may be distinguished by the position of the lateral tooth and the shape of the elytra, the latter being usually narrower and more parallel-sided than those of the *dentatus* group (see fig. 7).

Male genitalia.—The parameres are long and strongly tapering, resembling those of *labilis*, and, to a lesser extent, *intermedius* and *subdepressus*. The parameres of *cylindrus*, as figured by Bruce, are shorter, broader, and less strongly tapering. The aedeagus is of the *dentatus* type, resembling that of *subdepressus*.

Habitat.—Like *subdepressus*, apparently associated with coniferous trees.

The *dentatus* Group.

The *dentatus* group of sibling species has long caused confusion in the genus. We have so far recognised the following components: *dentatus* (Herbst), *pseudodentatus* Bruce, *acuminatus* sp. n., *rotundatus* sp. n., *intermedius* Bruce, and *inaequalis* Reitter. The last named has not yet been recognised in Britain. The first important step towards distinguishing these species was taken by Bruce, when he pointed out that the *pallidus* of Reitter and most authors was not the *pallidus* of Sturm. Sturm's species was closely related to *scanicus* and *postpositus*, whereas the *pallidus* of Reitter was hardly separable from *dentatus*. Bruce therefore assigned the appropriate name of *pseudodentatus* to this species.

At the start of our investigation we were soon satisfied that a number of *dentatus*, *pseudodentatus* and *intermedius* could be reliably recognised on external characters. There were, however, many specimens which were not immediately recognisable as any of these species, though obviously very close to all. When the male genitalia of these specimens were examined many proved to be atypical examples of one of them. Some, however, possessed parameres which differed from those of *dentatus*, *pseudodentatus* and *intermedius* to an extent equal to, or greater than, the difference between the parameres of most other species of *Cryptophagus*, but the aedeagi were almost identical. Among these individuals two distinct paramere forms predominated. Each form was quite constant in structure, and series of similar specimens from the same locality were found. For example, the form we have named *acuminatus* was first found in Mr. P.

Harwood's collection. A series of twenty-one specimens was labelled "dead alders, Nethy Bridge, 13.viii.29", and this series included ten males. Of these, two were *pseudodentatus* and the remainder *acuminatus*. All the females appeared to be *acuminatus*. Also a series of "*dentatus*" from Leyton, London, taken on 8.i.51 by Mr. R. D. Weal, included five male *rotundatus*. We consider that these two forms are sufficiently distinct in paramere structure to justify their description as species.

The few remaining variants in paramere structure were not constant among themselves, and we therefore give them no formal status, but three are illustrated (fig. 50) so that further examples may be recognised. It is possible that they may be hybrids between the other species. The *dentatus* group is obviously a complex of incipient species, some of which have differentiated to a greater extent than others. It is very likely that occasional hybridisation occurs within such a group.

We give below descriptions of the typical forms of each of the five species. Atypical forms occur commonly, and cannot be distinguished except on male genitalia. The descriptions of *rotundatus* and *acuminatus* are based upon the two series mentioned above, from which types have been selected and deposited at the British Museum (Natural History).

C. dentatus (Herbst) (= *fumatus* Marsham). (Figs. 32, 49a, b, c, 7b, c;
♂ Figs. 67, 110.)

Unicolorous red-brown, elongate, punctured, pubescent. Head strongly and moderately densely punctured; eyes with fine facets. Pronotum at least as broad as the base of the elytra, commonly conforming to one of the following three descriptions:

(1) Appearing almost quadrate, as broad across the callosities as across the lateral teeth; sides concave between callosity and lateral tooth, which is well in front of the midpoint of the sides, and strongly angled at the tooth, converging thence to base in an almost straight line (fig. 49 (b)).

(2) Appearing slightly transverse, and broader than the base of the elytra, broader across the lateral teeth than across the callosities; lateral tooth only slightly in front of the midpoint of the sides; sides strongly angled, converging from tooth to callosity as well as from tooth to base (fig. 49 (a)).

(3) Appearing quadrate, almost parallel-sided, very convex between the lateral margins; lateral tooth usually somewhat in front of the midpoint of the sides (fig. 49 (c)).

The pronotal puncturation in all three forms is highly variable, but usually much stronger and denser than the elytral puncturation. Elytra rather narrow and parallel-sided; pubescence simple, decumbent. Length 2.0-3.0 mm.

C. pseudodentatus Bruce. (Figs. 34, 49 (f); ♂ Figs. 71, 113.)

As *dentatus* except as follows:

Pronotum somewhat transverse, narrower than the base of the elytra; lateral tooth usually only slightly in front of middle of side; sides evenly rounded from callosity to base or slightly angled at lateral tooth, seldom strongly concave between callosity and tooth. Elytra rather parallel-sided, but often shorter and broader than in *dentatus*; pubescence rather longer and coarser. Length 2.0-2.8 mm.

C. acuminatus sp. n. (Figs. 33, 49 (e); ♂ Figs. 69, 112.)

As *dentatus* except as follows:

Pronotum appearing somewhat transverse, only slightly narrower than the base of the elytra; lateral tooth at or slightly in front of the middle of side; sides evenly rounded or

slightly angled at tooth and slightly concave between callosity at tooth. Elytra rather long, longer than *pseudodentatus*, but with sides more rounded, and disc convex, tending rather towards *fallax* in shape (fig. 3); pubescence fine and short. Length 2.4-3.0 mm.

C. rotundatus sp. n. (Fig. 49 (d); ♂ Figs. 68, 111.)

As *dentatus* except as follows:

Pronotum appearing quadrate or slightly transverse, slightly narrower than the base of the elytra; lateral tooth at or in front of middle of side; sides slightly angled at tooth, converging thence to base. Pubescence of pronotum rather conspicuous—long, yellowish, rather coarse. Elytra rather less rounded and convex than *acuminatus*, but more so than *dentatus*. Elytral pubescence similar to that of *pseudodentatus*. Length 2.3-2.8 mm.

C. intermedius Bruce. (Fig. 31; ♂ Figs. 74, 118.)

One form of this species (fig. 31) has a large callosity, strongly angled sides and the lateral tooth at the midpoint. A second has the callosity smaller, sides almost straight, pronotum very convex between the sides, and lateral tooth at, or in front of middle. Both have rather fine and moderately diffuse pronotal puncturation, and elytral puncturation which differs from it rather less than in other *dentatus* group species.

Male genitalia.—As has already been stated, the species of the *dentatus* group, and certain other closely allied species (e.g. *angustus*), possess aedeagi which are closely similar in structure, and quite distinct from those of most other species. The most characteristic feature is the preputial sac which appears as a conspicuous, horse-shoe-shaped structure of granular texture, with a cap at its apex. Similar structures may often be discerned in other aedeagi, but they are never conspicuous except in those species in which the aedeagus is described as *dentatus* type. In the *dentatus* group the cap is formed by three well-defined lines, one transverse, forming a tangent at the apex of the "horse-shoe", and the others obliquely on either side. The oblique lines form the outer sides of two small triangles which are granular in texture, and are separated by a clear triangle, the base of which is formed by the transverse line. These structures are associated with the orifice of the preputial sac and are present in all *dentatus* type aedeagi, but there is some variation in the degree of definition of the parts in different species. In *subdepressus* the lateral granular triangles are the most conspicuous feature of the aedeagus. In this species and also in *angustus*, the aedeagus is shorter than in the *dentatus* group, except *intermedius*, in which it is also short. The aedeagus of *pseudodentatus* possesses one feature not shown by other species in the group. When first dissected out the lateral parts are suffused with dark brown. This coloration appears to have no structural basis, and is less obvious in permanent preparations, but appears to be fairly constant, and is very conspicuous in a fresh aedeagus. Most of our preparations of *rotundatus* aedeagi show a small triangular fold on each side at the apex. This feature is not absolutely constant, and very occasionally occurs in other species of the group, but it is, in general, rather characteristic of *rotundatus*.

The parameres of the five *dentatus* group species are the only structures upon which a reliable separation can be based. Their chief characteristics are given below.

dentatus (fig. 67).—Elongate, but broadly rounded apically, the area of setate pores as large as, or larger than the area of asetate pores; basal emargination completely enclosed, appearing as an aperture in the base of the paramere. Large

apical setae numerous, usually more than six ; surface setae numerous but only moderately dense.

pseudodentatus (fig. 71).—Elongate, straight sided, the sides converging evenly towards the broadly rounded apex, the area of setate pores larger than the area of asetate pores. Base of paramere simple, without struts or emargination, but with a small thickening and fold at the base of the median margin. Large apical setae usually four ; larger surface setae usually forming a transverse row of three near the apex ; small surface setae not numerous, diffuse.

acuminatus (fig. 69).—Elongate, tapering, the area of setate pores approximately equal to the area of asetate pores. A narrow, tapering chitinous strut passes from the lateral margin across the base of the paramere, leaving a considerable gap between its apex and the base of the median margin. Large apical setae usually two or three ; medium sized setae often extending along the lateral margin towards the base ; surface setae very dense near the apex of the basal strut.

rotundatus (fig. 68).—Very short, oval, the area of setate pores much smaller than the area of asetate pores. A thick, rounded chitinous strut passes from the lateral margin across the base of the paramere, but does not meet the median margin. Large apical setae usually two or three ; surface setae numerous and very dense.

intermedius (fig. 74).—Elongate, evenly tapering, the area of setate pores about equal to the area of asetate pores. Base appearing enclosed, but without emargination. Large apical setae usually two, rather short. Larger surface setae in a longitudinal row of five or six near the apex. Smaller surface setae few, very sparse towards the base.

Of the parameres which do not conform to any of these descriptions, three are illustrated in fig. 50. The presence of two lines separating the areas of setate and asetate pores is a feature of these parameres, although they differ from one another in other respects. Others approximate more closely to the named species.

Habitat.—In view of the confused position in the *dentatus* group, little information about habitat preferences can be given. The various species are frequently found together, but we have noticed that *dentatus* sometimes occurs in fungi and that *pseudodentatus* is often abundant in haystacks, unaccompanied by other species of the group. Three species, *dentatus*, *pseudodentatus* and *rotundatus*, have been found in warehouses, etc. Bruce gives no information as to the habitat of *intermedius*, but one example (determined by Mr. S. Shaw of the Manchester Museum) was taken at sycamore sap by Dr. W. D. Hincks at Thornton-le-Dale, Yorks, on 20. iv. 52.

C. corticinus Thomson. (Fig. 36 ; ♂ Figs. 78, 122.)

This species is closely allied to the *dentatus* group. The pronotum is rather flat, resembling *subdepressus* in this respect, but the sinuate sides are very characteristic.

Male genitalia.—The aedeagus resembles that of the *dentatus* group, but shows, in addition, structures rather similar to, but much less conspicuous than, those of *setulosus*.

Habitat.—We discovered the first British specimens in the collection of Mr. P. Harwood, labelled "burnt birch, Aviemore, 14. viii. 43" and have found occasional individuals in other collections. Bruce states that it is a northern species.

C. subvittatus Reitter. (Fig. 37; ♂ Figs. 79, 123.)

Close to *hexagonalis*, but not difficult to separate from the typical colour form of that species.

Male genitalia.—We have not seen a male of this species. The figures are taken from Bruce.

Habitat.—The only British example we have seen was a female, taken in a London dock-side warehouse in November, 1952, by Miss M. W. Howroyd of the Infestation Control Division (London Area) of the Ministry of Agriculture and Fisheries.

C. hexagonalis Tournier. (Fig. 38; ♂ Figs. 80, 124.)

The pubescence of this species is long and uneven, and might possibly be considered double, though we regard it as single. Bruce remarks upon this feature, but also places *hexagonalis* in the single-pubescence group.

Habitat.—We first recognised this species in the British Museum collection, where there were six specimens, accompanied by two *rotundatus*, labelled "on new oak in B.M.". Recently Mr. B. J. Southgate, of this Laboratory, made a small collection of *Cryptophagus* in a London dock-side warehouse, and, among many examples of common species, we recognised two *hexagonalis*. There are also two examples in the Manchester Museum collections.

C. postpositus Sahlberg. (= *hirtulus* Kraatz partim). Fig. 39; ♂ Figs. 75, 119.)

As is apparent from the key, we have had great difficulty in finding constant and distinct characters upon which to separate the four species *postpositus*, *badius*, *pallidus* and *scanicus*. In fact, these species provide an excellent example of the point made earlier in this paper, that the general form of the pronotum as a whole is often a more reliable taxonomic feature than the individual characters of the pronotum which contribute to this general appearance. All characters which appear to be useful have been included in the key, but no single feature is completely constant.

This close similarity has caused much confusion in the past. The species we now know as *pseudodentatus* was misidentified as the *pallidus* of Sturm, while the true *pallidus* Sturm, together with *postpositus* Sahlberg, was determined as *hirtulus* Kraatz. In Britain, Joy, whose *pallidus* was *pseudodentatus*, discovered the true *pallidus* and named it *fowleri* Joy. Thus we have:

postpositus Sahl. = *hirtulus* Kr. partim.

pallidus Sturm = *hirtulus* Kr. partim = *fowleri* Joy.

pseudodentatus Bruce = *pallidus* auctt. nec Sturm.

There are very few records of *hirtulus* in Britain. The only one we have seen (Power coll.) was a *postpositus*. The *pallidus* component was usually separated as *fowleri* Joy, and *postpositus* was almost invariably misidentified as *badius*.

Habitat.—General.

C. badius Sturm. (Fig. 40; ♂ Figs. 76, 120.)

This species has already been discussed under *fallax* and *postpositus*. It is excessively rare in Britain, all previous records referring to *postpositus*, *pilosus*,

or some other species. The only British examples known to us were taken from a squirrel's drey at Aviemore, Inverness, by Mr. P. Harwood (see under *lapponicus*). The specimens standing as *badius* in British collections comprise many species, but two generally predominate—*postpositus* and "short-haired" *pilosus*. Confusion with *postpositus* is not surprising, as the species are very close, but confusion with *pilosus* is not easy to understand. It is doubtless due to the wide use of Fowler (1886-91; 1913) by British coleopterists. In Vol. 6 (1913, p. 128) he describes the close similarity of *badius* and *pilosus* and states that his opinion, expressed previously in Vol. 3 (1886-91, p. 316), that *pilosus* was the commoner of the two, was incorrect and that he now regarded *badius* as commoner than *pilosus*. Failure to appreciate the variation of pubescence in *pilosus* undoubtedly contributed to this misunderstanding.

Bruce (1936) emphasises the difficulty of recognising *fuscicornis* Sturm, and states that many examples are hardly separable from *badius*. His figures of the parameres of the two species show that considerable differences exist between them, differences which he emphasises in the text (p. 87). We have, however, already pointed out (see under *fallax*) that, whereas Bruce's figures of the parameres of *fallax* and *quercinus* agree closely with those we have seen, his figure for *badius* differs somewhat from all the preparations we have studied. Moreover, two male specimens of *badius* supplied by Bruce, and a slide of *fuscicornis* genitalia from his collection, all showed parameres similar to those obtained from British specimens of *badius*. These *badius* parameres are rather intermediate between Bruce's figures for *badius* and *fuscicornis*, though closest to the former. Bruce describes his drawing of *fuscicornis* genitalia as based upon the "Typenpreparat" so we cannot dispute that the species exists. However, there can be little doubt that it must be deleted from the British list.

Habitat.—The only authentic British specimens were taken from a squirrel's drey as described above.

C. pallidus Sturm (= *fowleri* Joy, = *hirtulus* Kraatz partim).

(Fig. 41; ♂ Figs. 81, 125, 127.)

The confusion which has, in the past, surrounded this species has already been dealt with under *postpositus* and *pseudodentatus*. It is closest to *scanicus* and cannot be distinguished with certainty on external features from certain unicolourous examples of that species.

Habitat.—General.

C. scanicus L. (Fig. 42; ♂ Figs. 66, 109.)

The characteristic coloration of the typical form is a useful guide in separating this species from its allies. The unicolourous form (var. *patruelis*) is very close to *pallidus*.

Habitat.—General. It is probably the commonest outdoor species in Britain.

VII. NOTES ON THE SPECIES OF *MICRAMBE* THOMSON.

M. bimaculatus Panzer. (Fig. 46; ♂ Figs. 87, 93.)

This species is quite unlike any other in the genus, and cannot be assigned satisfactorily to any of the three subgenera, though it is nearest to *Micrambe*.

Male genitalia.—At each side the apex of the aedeagus is produced into a large, triangular flap which meets its fellow in the mid-line. No similar structure is present in any other species.

Habitat.—According to Bruce it is associated with coniferous trees. It is very rare in Britain.

M. vini Panzer. (Fig. 44 ; ♂ Figs. 86, 89.)

This species is distinct from *villosus* Heer and is not a synonym of that species, as given by Kloet and Hincks (1945). The two species are separated in most keys by the presence of double pubescence in *villosus* as opposed to single in *vini*. This is not a satisfactory separation, for some examples of *vini* possess double pubescence, though we have not found any *villosus* with single pubescence. Bruce states that in *villosus* the eyes are less prominent, the head is larger, the pronotum more transverse, and the elytra are shorter and more convex than in *vini*. We have been unable to use these features, either singly or in combination, to separate the two species and consider that "long-haired" *vini* can be distinguished from *villosus* only by examination of the male genitalia. These, however, are very distinct.

Male genitalia.—The parameres of *vini* are very small, being only about half as long as those of *villosus*. The long acuminate lateral portions of the aedeagus may be deflected towards the mid-line as in fig. 89 (a) or may, especially before mounting, project as in fig. 89 (b).

Habitat.—Usually associated with gorse (*Ulex*) and broom (*Cytisus*).

M. villosus Heer. (Fig. 45 ; ♂ Figs. 88, 90.)

See under *vini* and *lindbergorum*.

Male genitalia.—The aedeagus is similar to that of *vini*, but the endophallus shows one conspicuous and unusual feature—a group of large, strong teeth (fig. 90). Very occasionally, in both this and the previous species, it is possible to discern faint traces of the heart-shaped structure which is so conspicuous in *abietis* and *lindbergorum*.

Habitat.—Possibly similar to *vini*, but this is uncertain because of the confusion of the two species.

M. abietis Paykull. (Fig. 48 ; ♂ Figs. 84, 91.)

On the basis of pronotal shape, this species is closest to *aubrooki*, but may be readily separated as in the key. It should be noted that the hind tarsi of the male are five-segmented.

Male genitalia.—The genitalia of this species are very close to those of *lindbergorum*, but distinct from other species of *Micrambe*. The parameres of *abietis* narrow more abruptly close to the base, the structures thus appearing longer and thinner than in *lindbergorum*. The large apical setae equal the paramere in length in the latter species, but are only about two-thirds of its length in *abietis*. Also, in all specimens we have examined, there is a row of four larger surface setae in *lindbergorum*, but only three are present in *abietis*. In both species the aedeagus shows a complex, heart-shaped structure which is very conspicuous. There are also two large, elongate bodies lying obliquely at the extreme base of the apodeme. Such slight differences as exist between the aedeagi of the two species are illustrated in the figures, but comparatively

few examples of either have been examined, so these differences may not be constant.

Habitat.—Associated with coniferous trees.

M. lindbergorum Bruce. (Fig. 43 ; ♂ Figs. 85, 92.)

In general, this species is intermediate between *abietis* and *villosus*. Like the latter, it possesses double pubescence, but the pronotum is slightly less transverse and the callosities are rather less prominent.

Male genitalia.—Almost identical with *abietis* (see above).

Habitat.—The only British examples, two males, were taken by sweeping at Spurn Head, Yorks., by Dr. W. D. Hincks, one on 15.viii.49 and the other on 26.vii.53.

M. aubrooki Donisthorpe. (Fig. 47.)

Closest to *abietis*, but distinguished by the rather strong, diffuse pronotal puncturation. In *abietis* the pronotum is rather finely and very densely punctured.

Male genitalia.—Unknown.

Habitat.—The type specimen, the only example hitherto known, was taken at a flower show at Manchester in November, 1934. There is, also, in the British Museum, a female *Micrambe* which seems to us to be this species. It bears a locality label "Vigo, N.W. Spain. G.C.C." and a Bruce determination label "*nec vini, nec villosus*".

VIII. SUMMARY.

The value of existing keys for identifying British species of the genus *Cryptophagus* Herbst is briefly considered.

Following Reitter (1908-16) and Bruce (1936) *Micrambe* Thomson and *Mnionomus* Wollaston are considered to be subgenera of *Cryptophagus* (Herbst).

The various external morphological characters which are commonly used in keys to the species of *Cryptophagus* are discussed with reference to their reliability. The general form of the pronotum and the structure of the pronotal callosity are considered to be the most reliable external characters. The pronotum of every British species is illustrated.

The taxonomic value of the characters of the male genitalia is stressed. Drawings are given of parameres and aedeagus of all British species. The method used in preparing slides of the genitalia is described.

The various terms used in the keys are defined and explained.

Keys are given to the subgenera of *Cryptophagus* Herbst ; to the species of *Cryptophagus* s.str. (including *Mnionomus* Wollaston); and to *Micrambe* Thomson. The component species of the *dentatus* group are not separated in these keys.

General and comparative notes, and notes on the male genitalia, together with information concerning habitat, are given for each species. Altogether, including those about which notes have already been published, the list includes two species described for the first time, eight species new to Britain, eight species hitherto widely misidentified in this country, and one deleted from the British list.

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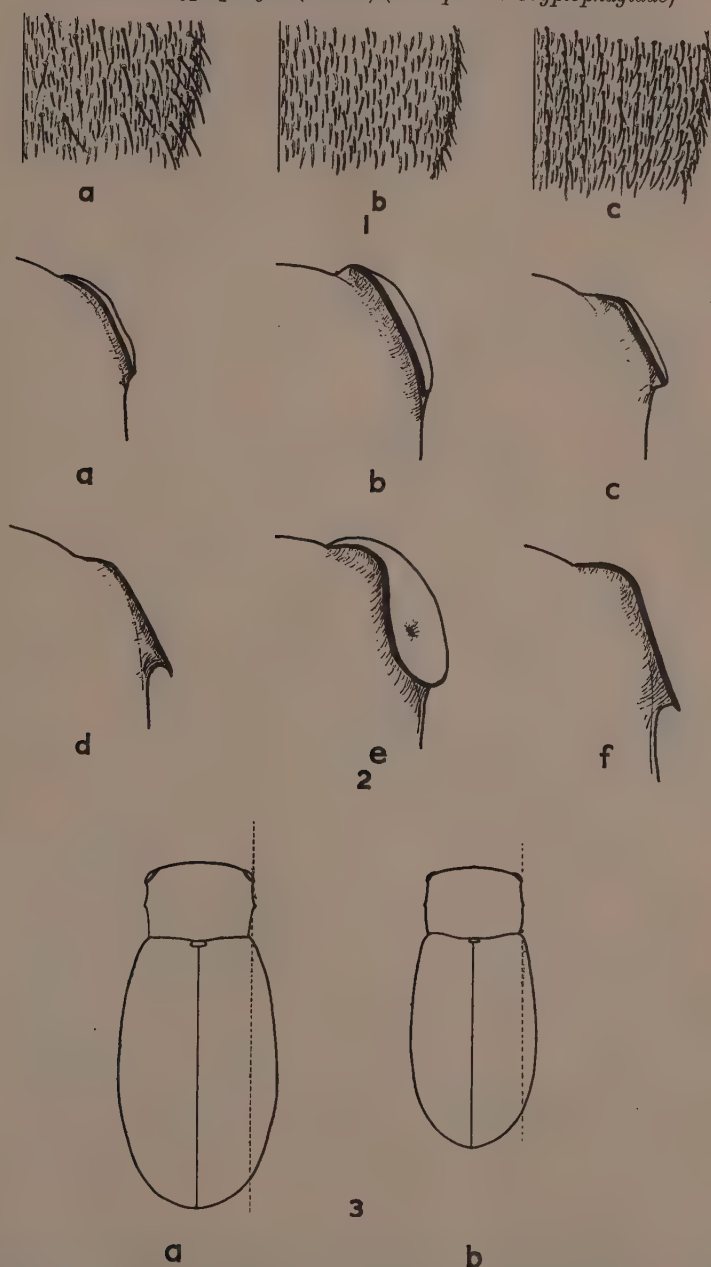
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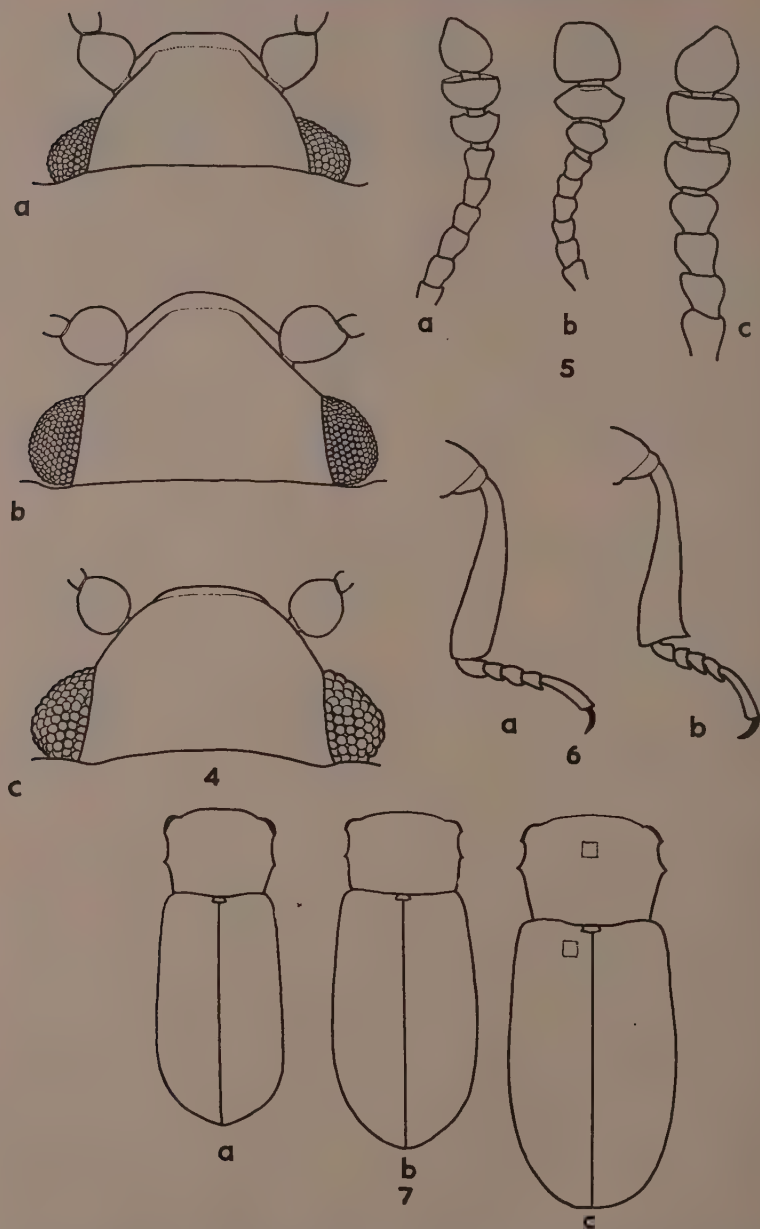
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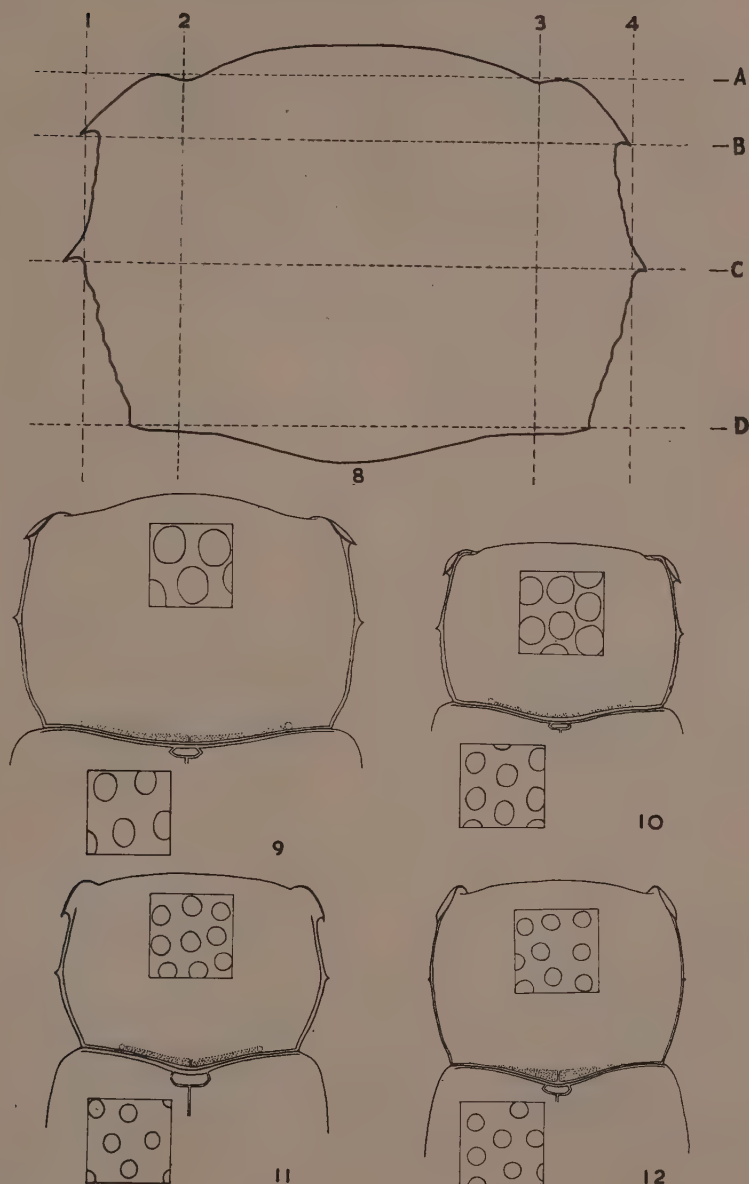
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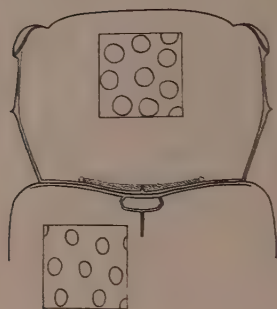
FIGS. 1-3.—(1) Elytral pubescence. (a) double; (b) single; (c) *cellaris* type double. (2) Callosities. (a)–(c) right-angled or obtuse-angled behind; (d) hook-toothed behind; (e) rim-toothed, upturned; (f) same viewed in plane of face. (3) Comparison of elytral shape. (a) *fallax*; (b) *acuminatus*.



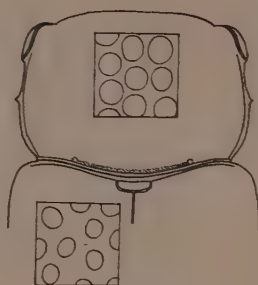
FIGS. 4-7.—(4) Eyes. (a) conical (*laticollis*); (b) normal; (c) large, with large facets (*cellaris*, *acutangulus*). (5) Antennae. (a) normal; (b) two-segmented club (*mica-ceus*, *pubescens*); (c) robust funiculus (*populi*). (6) Fore tibiae. (a) normal; (b) toothed (*lycoperdi*, *populi*). (7) Comparison of body form. (a) *angustus*; (b)-(c) *dentatus*; (c) also shows the position of the illustrated areas of puncturation.



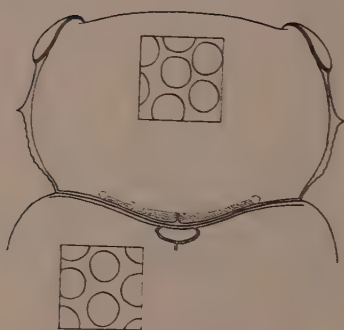
FIGS. 8-12.—(8) Measurements upon which proportions of pronotal characters are based (see text). (9)-(12) Pronotum and base of elytra ($\times 70$) with comparison of puncturation ($\times 175$). (9) *lycoepardi*. (10) *ruficornis*. (11) *pilosus*. (12) *simplex*.



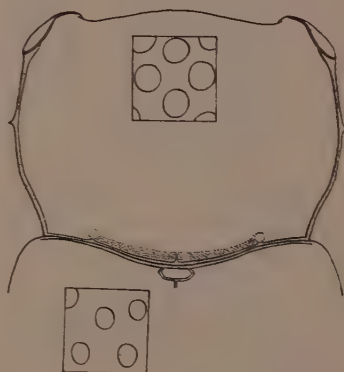
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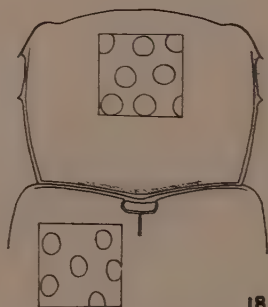
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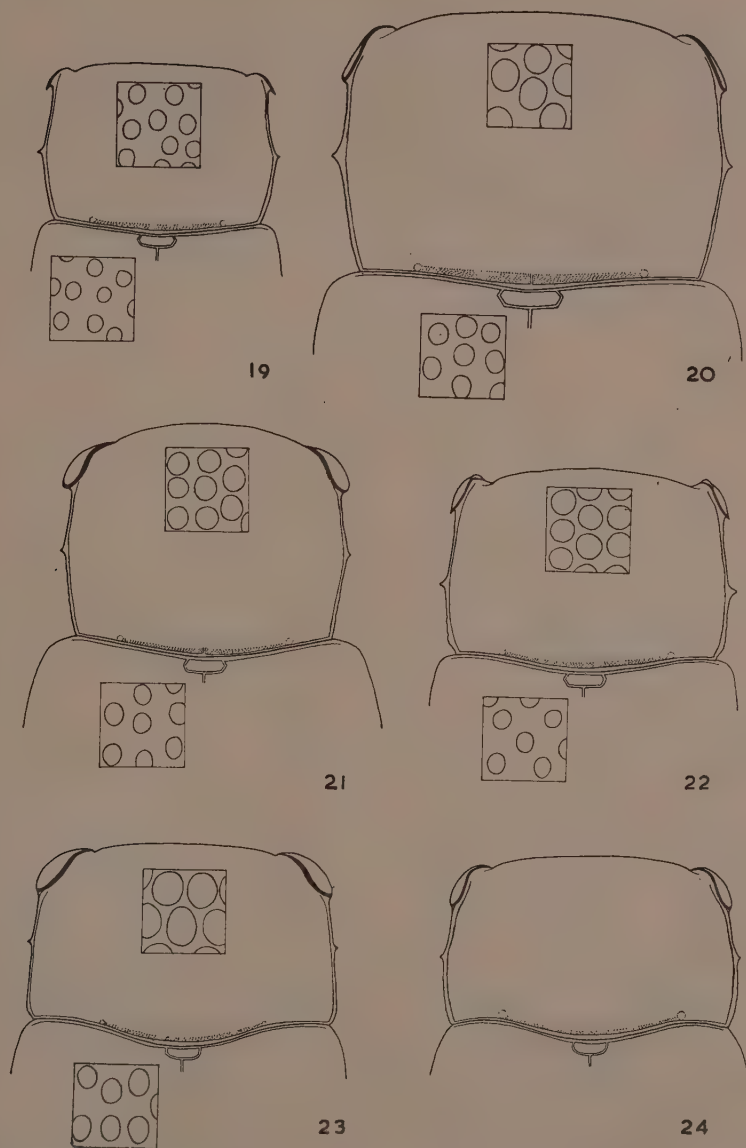


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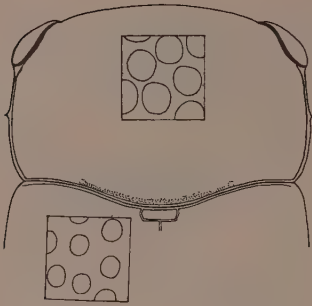


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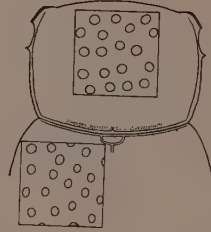
FIGS. 13-18.—Pronotum and base of elytra ($\times 70$) with comparison of puncturation ($\times 175$). (13) *cellaris*. (14) *laticollis*. (15) *setulosus*. (16) *schmidtii*. (17) *acutangulus*. (18) *labilis*.



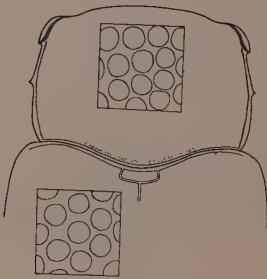
FIGS. 19-24.—Pronotum and base of elytra ($\times 70$) with comparison of puncturation ($\times 175$). (19) *distinguendus*. (20) *populi*. (21) *fallax*. (22) *obsoletus*. (23)-(24) *pubescens*.



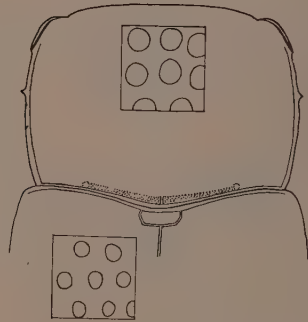
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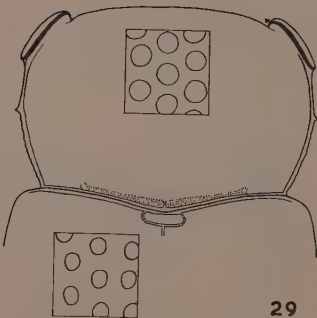
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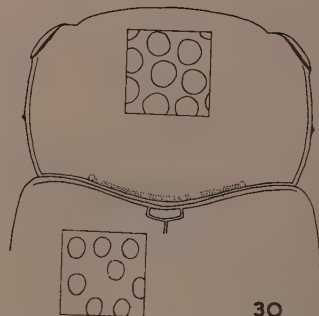
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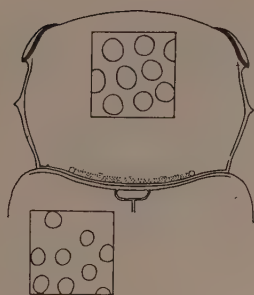


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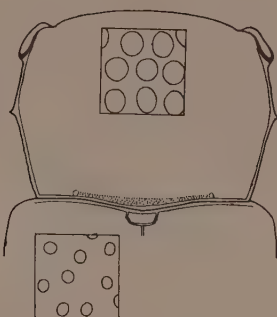


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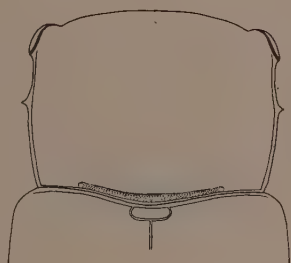
FIGS. 25-30.—Pronotum and base of elytra ($\times 70$) with comparison of puncturation ($\times 175$). (25) *micaceus*. (26) *scutellatus*. (27) *subdepressus*. (28) *saginus*. (29) *subfumatus*. (30) *lapponicus*.



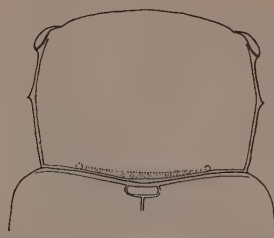
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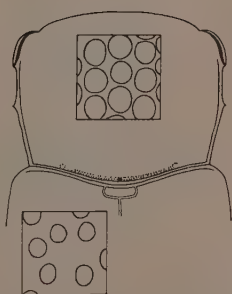
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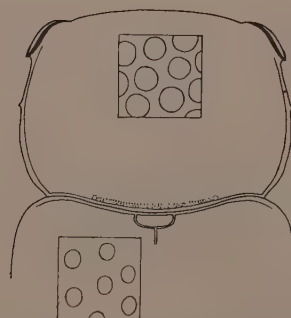
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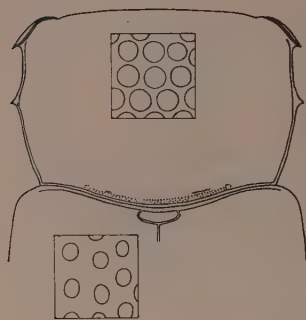


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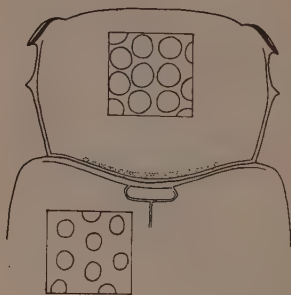


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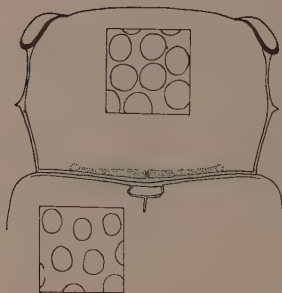
FIGS. 31-36.—Pronotum and base of elytra ($\times 70$) with comparison of puncturation ($\times 175$). (31) *intermedius*. (32) *dentatus*. (33) *acuminatus*. (34) *pseudodentatus*. (35) *angustus*. (36) *corticinus*.



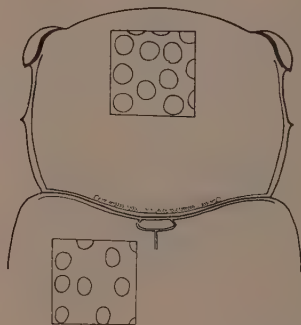
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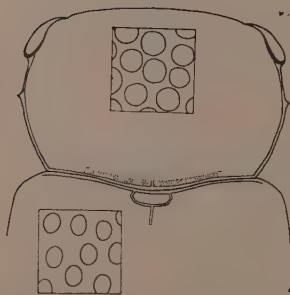
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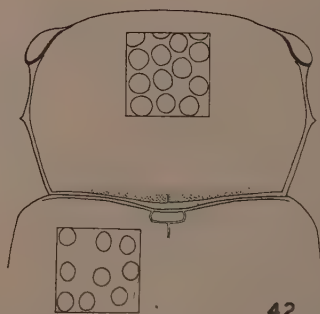
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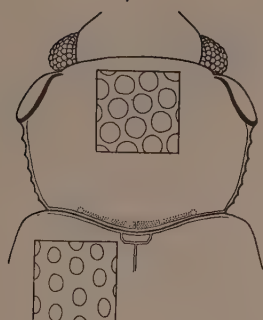


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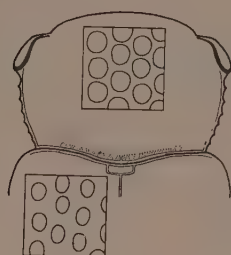


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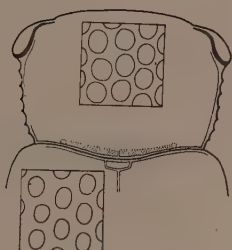
FIGS. 37-42.—Pronotum and base of elytra ($\times 70$) with comparison of puncturation ($\times 175$). (37) *subvittatus*. (38) *hexagonalis*. (39) *postpositus*. (40) *badius*. (41) *pallidus*. (42) *scanicus*.



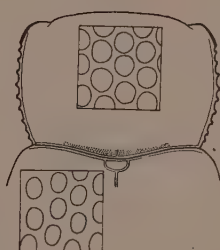
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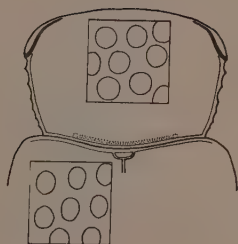
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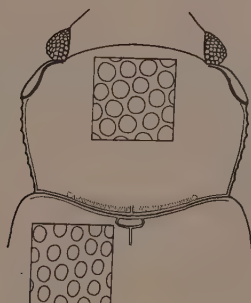
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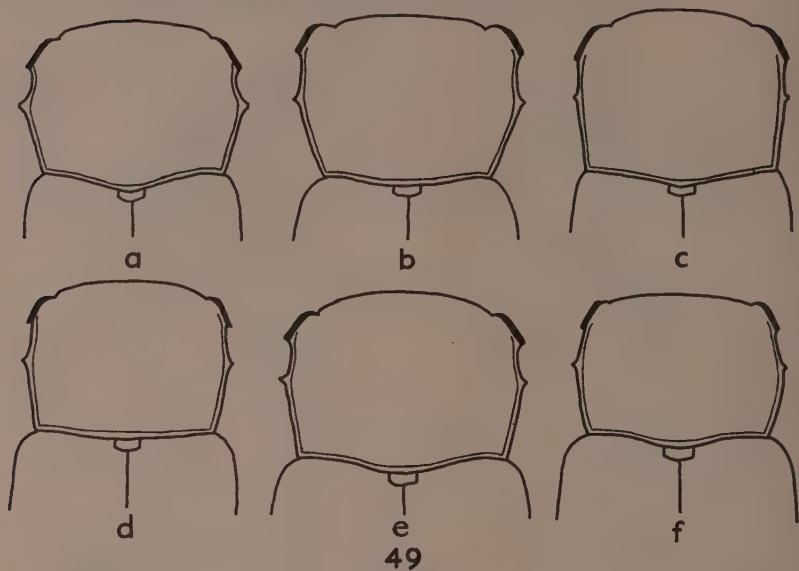


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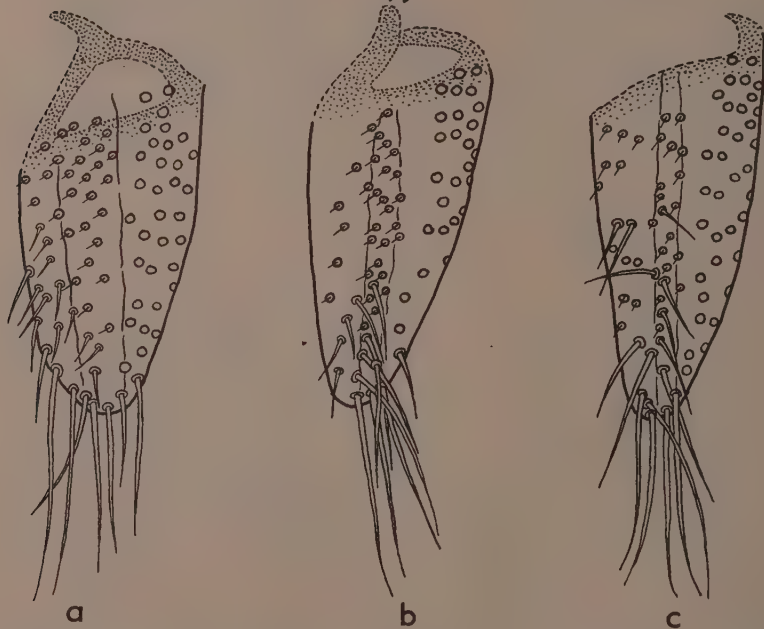


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FIGS. 43-48.—Pronotum and base of elytra ($\times 70$) with comparison of puncturation ($\times 175$). (43) *lindbergorum*. (44) *vini*. (45) *villosus*. (46) *bimaculatus*. (47) *aubrooki*. (48) *abietis*.



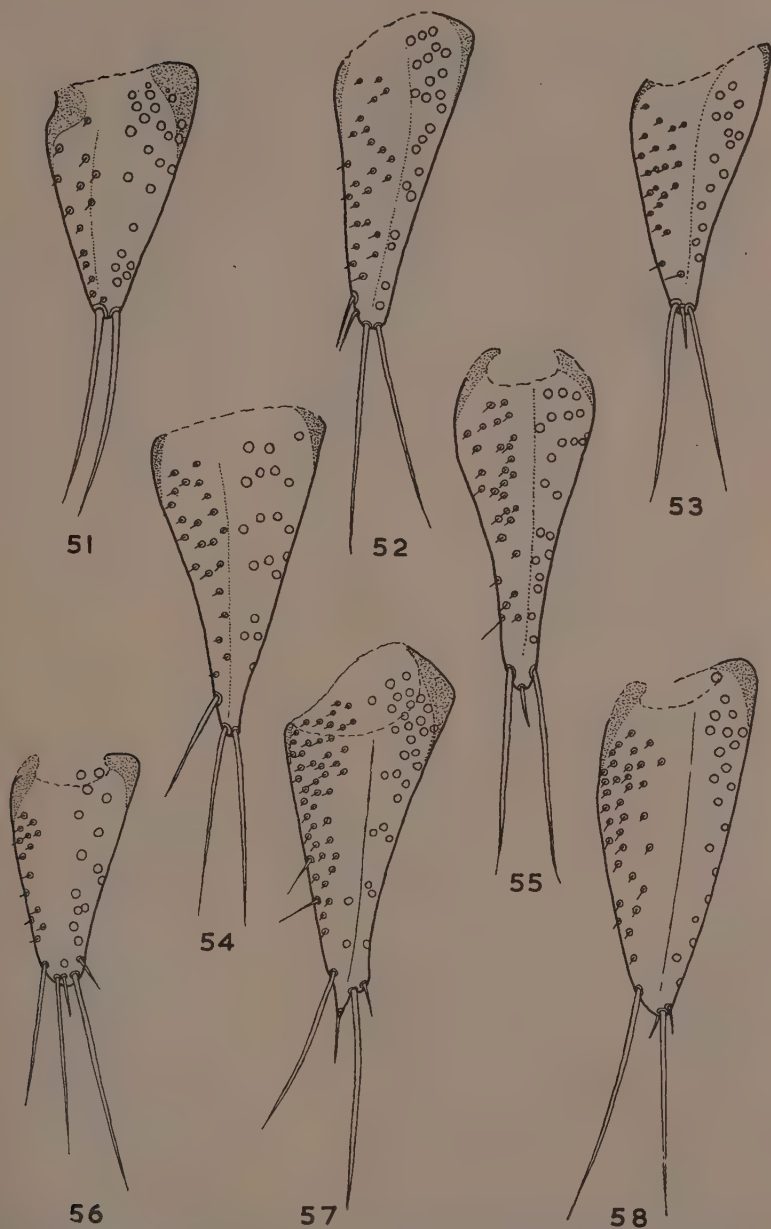
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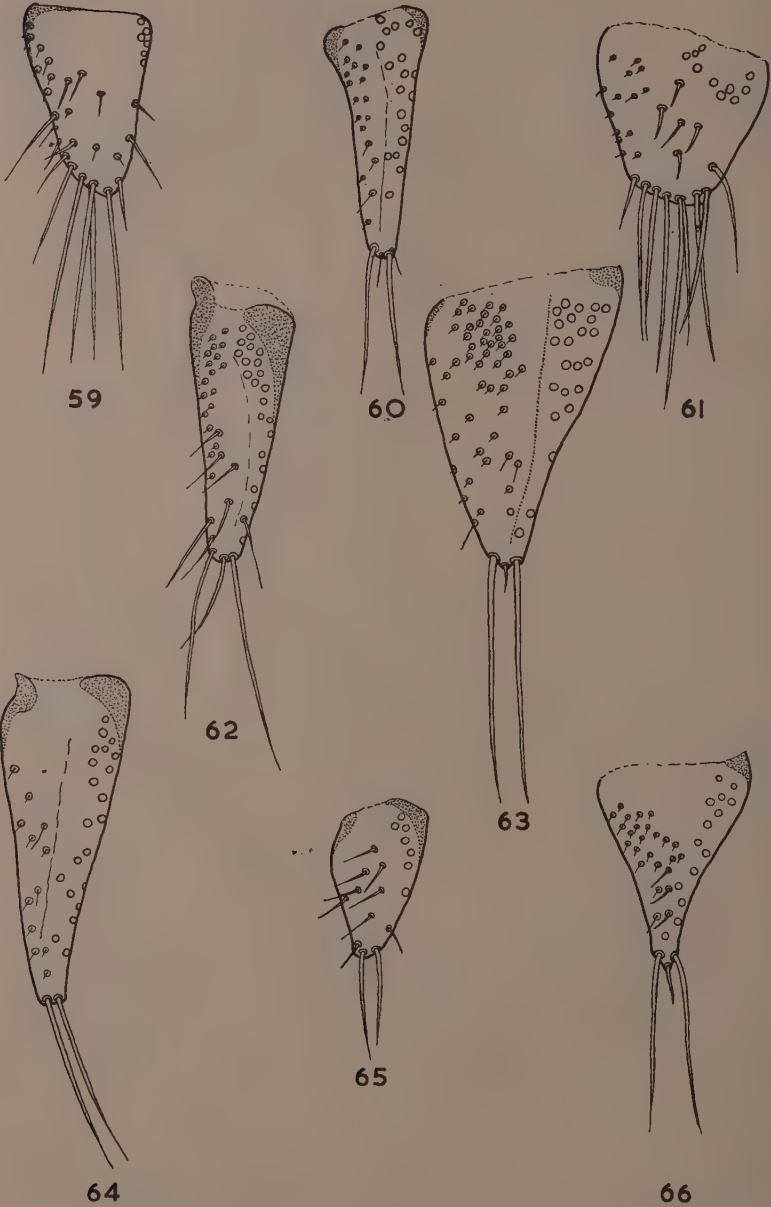
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FIG. 49.—Pronotum and base of elytra. (a)–(c) *dentatus*; (d) *rotundatus*; (e) *acuminatus*; (f) *pseudodentatus*.

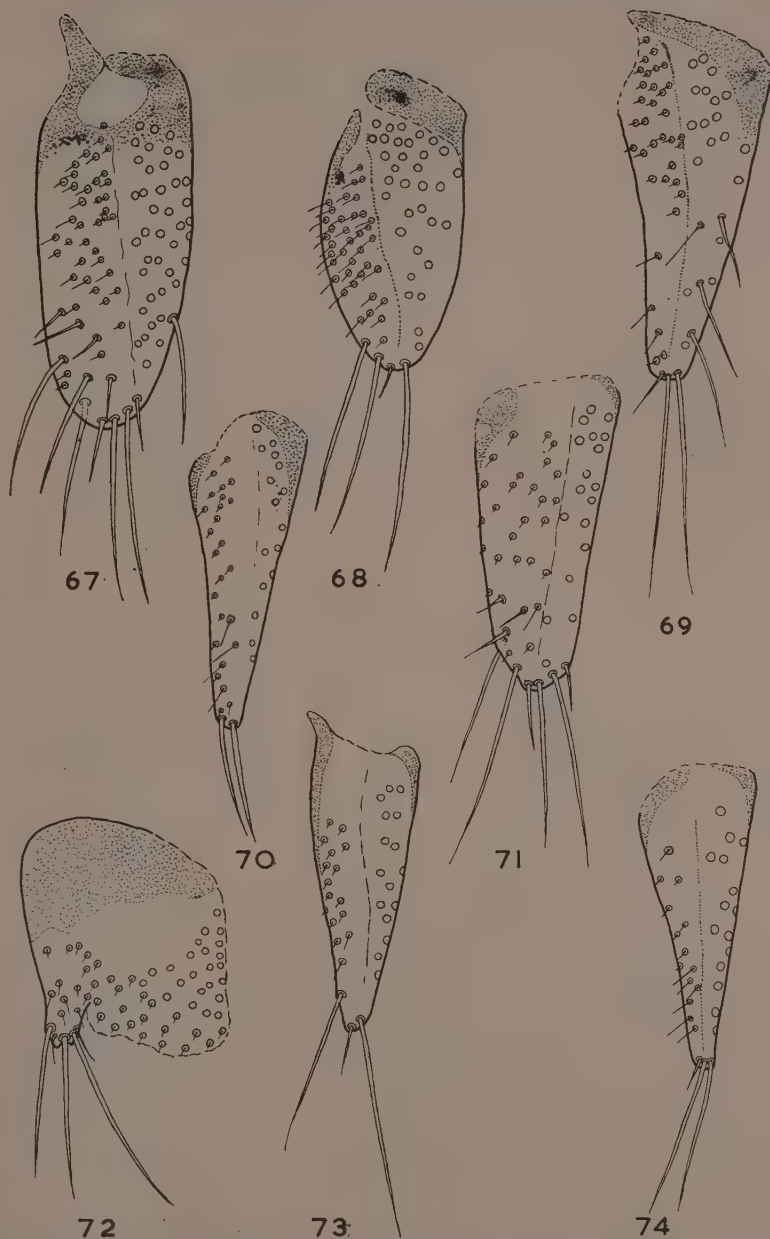
FIG. 50.—Three atypical parameres of *dentatus* group.



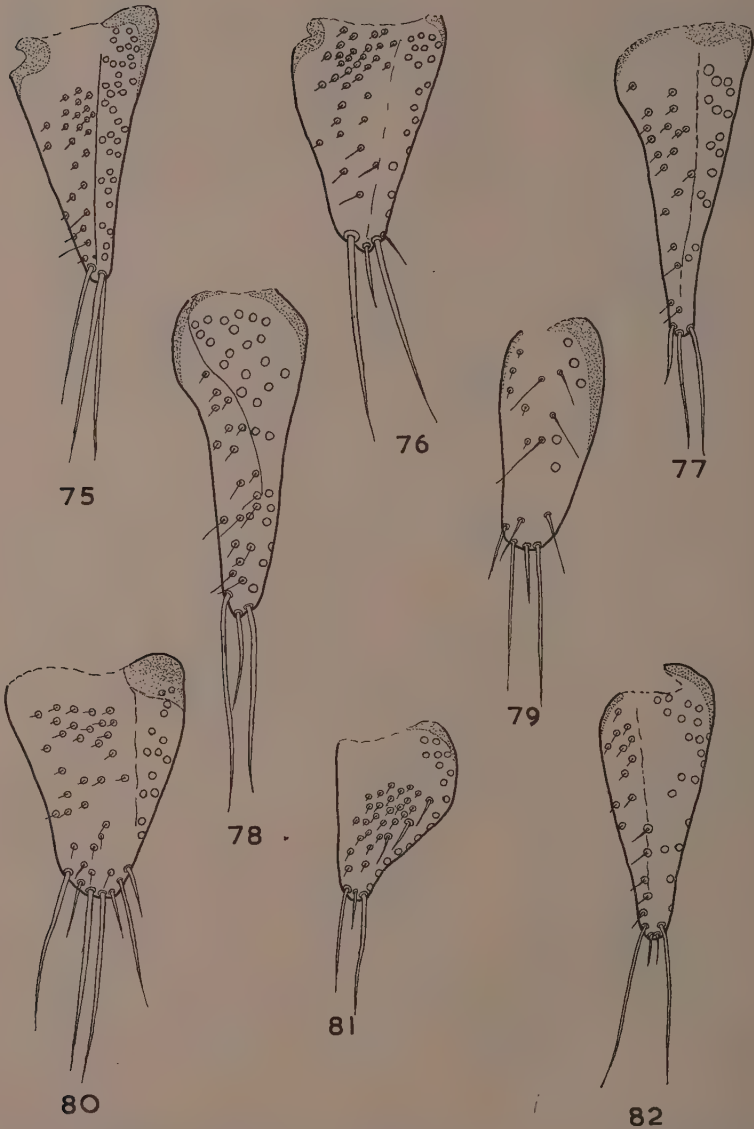
FIGS. 51-58.—Right paramere. (51) *lycoperdi*. (52) *ruficornis*. (53) *pilosus*. (54) *simplex*. (55) *cellaris*. (56) *laticollis*. (57) *setulosus*. (58) *schmidtii*.



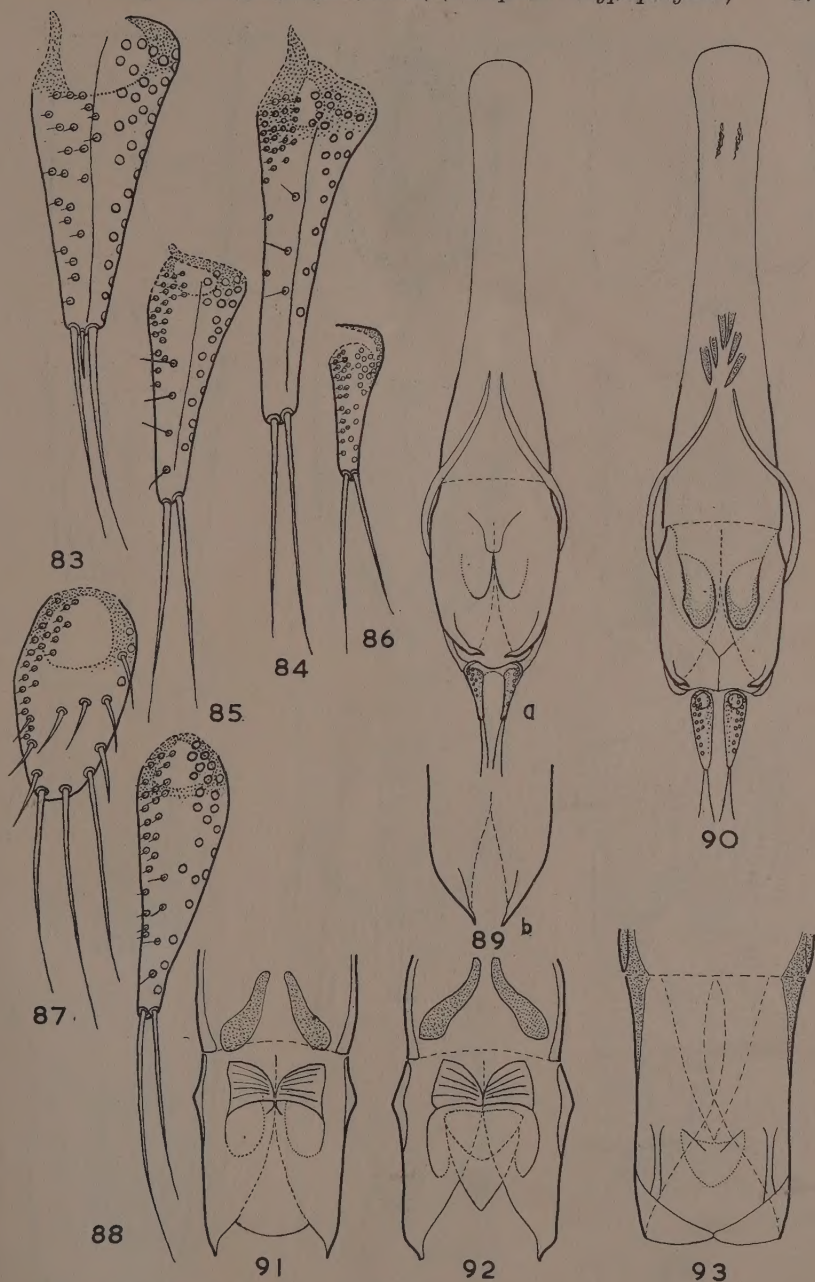
FIGS. 59-66.—Right paramere. (59) *acutangulus*. (60) *labilis*. (61) *distinguendus*. (62) *obsoletus*. (63) *fallax*. (64) *populi*. (65) *scutellatus*. (66) *scanicus*.



FIGS. 67-74.—Right paramere. (67) *dentatus*. (68) *rotundatus*. (69) *acuminatus*. (70) *subdepressus*. (71) *pseudodentatus*. (72) *subfumatus*. (73) *saginat*us. (74) *intermedius*.



FIGS. 75-82.—Right paramere. (75) *postpositus*. (76) *badius*. (77) *angustus*. (78) *corticinus*. (79) *subvittatus* (after Bruce). (80) *hexagonalis*. (81) *pallidus*. (82) *micaceus, pubescens*.

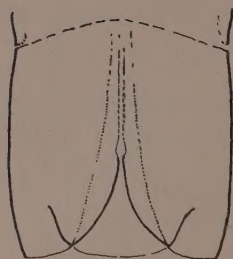


FIGS. 83-88.—Right paramere. (83) *lapponicus*. (84) *abietis*. (85) *lindbergorum*. (86) *vini*. (87) *bimaculatus*. (88) *villosus*.

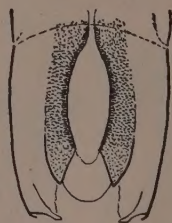
FIG. 89.—*vini*. (a) male genitalia; (b) alternative position of apex of aedeagus.

FIG. 90.—*villosus*. Male genitalia.

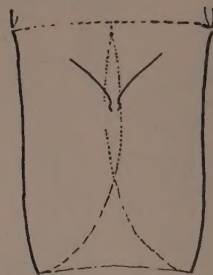
FIGS. 91-93.—Aedeagus. (91) *abietis*. (92) *lindbergorum*. (93) *bimaculatus*.



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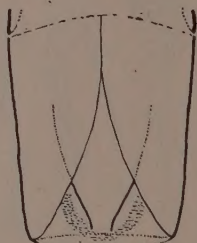
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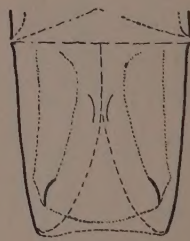
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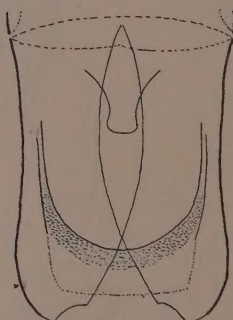
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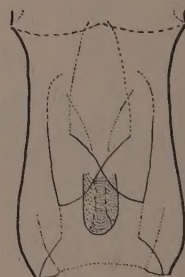
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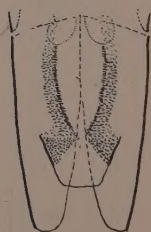
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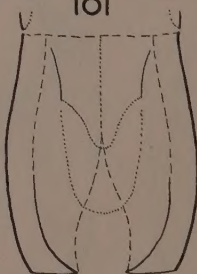
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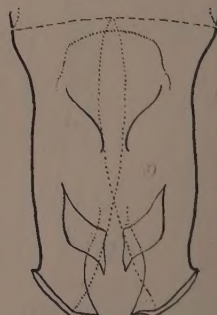
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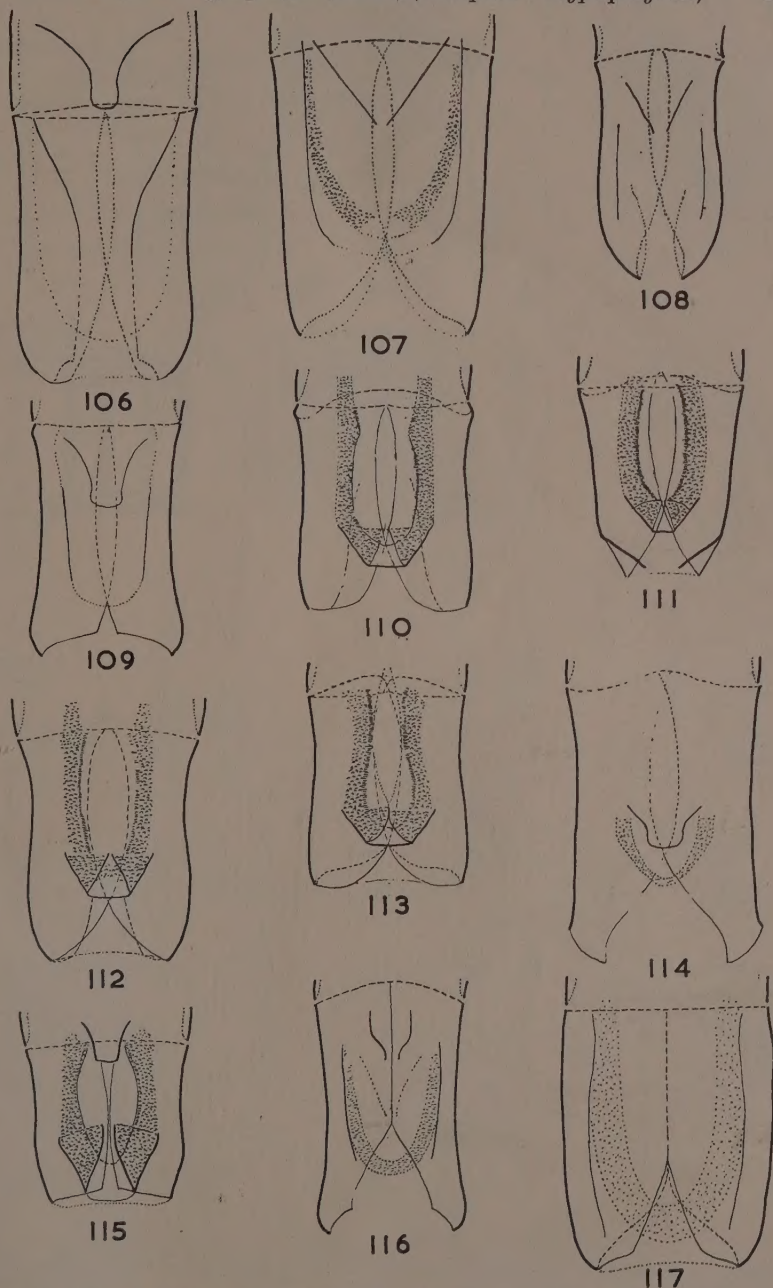


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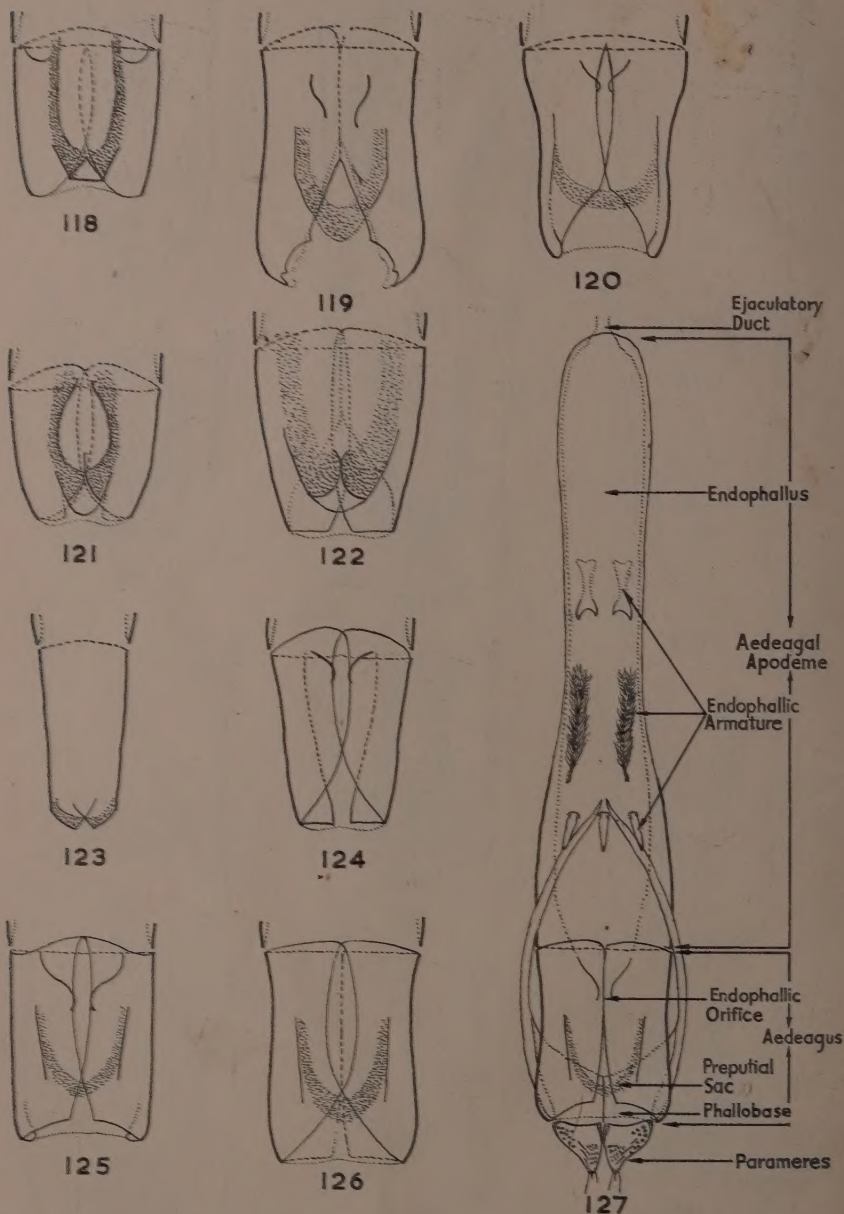


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FIGS. 94-105.—Aedeagus. (94) *lycoperti*. (95) *ruficornis*. (96) *pilosus*. (97) *simplex*. (98) *cellaris*. (99) *laticollis*. (100) *setulosus*. (101) *schmidti*. (102) *acutangulus*. (103) *labilis*. (104) *distinguendus*. (105) *obsoletus*.



FIGS. 106-117.—Aedeagus. (106) *fallax*. (107) *populi*. (108) *scutellatus*. (109) *scanicus*. (110) *dentatus*. (111) *rotundatus*. (112) *acuminatus*. (113) *pseudodentatus*. (114) *saginatus*. (115) *subdepressus*. (116) *subfumatus*. (117) *lapponicus*.



FIGS. 118-126.—Aedeagus. (118) *intermedius*. (119) *postpositus*. (120) *badius*. (121) *angustus*. (122) *corticinus*. (123) *subvittatus* (after Bruce). (124) *hexagonalis*. (125) *pallidus*. (126) *micaceus, pubescens*.

FIG. 127.—*pallidus*. Male genitalia.